Ontogenetic patterns of distribution in coral reef fishes, within the mangroves of a Caribbean atoll.

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Declaration

I hereby declare that this thesis has been composed by me and comprises my own work. Where information from other sources has been used it has been duly acknowledged. The work described in this thesis has not been submitted for any other degree or professional qualification.

Signed..... .....

Abstract

Mangroves are potentially important habitats for the early life stages of fishes, but their function as nursery grounds is not always apparent and remains unevaluated in many regions. The mangrove habitat is being lost at a rapid pace through deforestation, aquaculture and overexploitation of wood and fisheries resources, and current levels of use are unlikely to abate in the near future. As the pressure from population growth and development increases, a better understanding of mangrove ecosystem function is required in order to facilitate informed management decisions. This thesis aims to assess the relative importance of the mangrove forest within a Caribbean atoll, in the early life history stages of coral reef fishes.

Size frequency data were collected for fish assemblages within the mangrove prop-roots and adjoining seagrass beds of Calabash Cay, on the eastern rim of Turneffe Islands atoll, Belize, Central America. The atoll comprises a combination of numerous small sand cays, large mangrove cays and mangrove-sand cays, with coral patch reefs and extensive seagrass beds contained within the atoll lagoons. The area is largely unprotected by legislation and is steadily being developed, with four tourist resorts presently in operation. Fishing pressures are not well documented but several temporary and permanent fishing camps are in use throughout the atoll.

Three quantitative techniques were used. Stationary light traps and towed plankton nets collected larval stages, and a visual census technique was used to assess juvenile and adult stages. Environmental factors, including habitat structure, were measured simultaneously. The study was conducted over the months of August-September 2000 and June-November 2001. A nested sampling design provided the distribution of fish on three spatial scales, at 10s, 100s and 1000s of metres. A total of 159 species or types of coral reef fish within 50 families were recorded.

The proportion of species present as larvae, and therefore available to settle, was greater in the seagrass than in the mangroves. Twelve taxa present in all three life-cycle stages showed contrasting patterns of distribution between the seagrass and mangrove habitats, with 11 appearing to be open populations. The mean body size of each life stage was smaller in the seagrass than in the mangroves, indicating a preference for the mangrove habitat by larger and therefore older individuals. Diel movement between habitats is evident for the larval assemblage, with higher densities in the seagrass during the day and in the mangroves at night. Lunar periodicity was evident, with the greatest abundance, species diversity and species richness of larvae coincident with the three-quarter moon, and a high density also collected during the new moon. Tidal effects were minimal. Temporal variation in the larval assemblage composition correlated with water turbidity in both mangrove and seagrass habitats. The mangrove larval population was related to both the mangrove and the seagrass adult populations, and reflected the larval supply with a time lag of 2 to 4 weeks. Overall juvenile density reflected the larval supply density, with a time lag of two months. The recruitment of *Ocyurus chrysurus* and members of the family Scaridae, especially *Sparisoma* sp., was related to the respective spawning stocks in the mangrove and seagrass habitats. The densities of *Haemulon flavolineatum* and *Lutjanus griseus* juveniles decreased as the structural complexity of the mangrove habitat increased, while the relative abundance of larger, older juveniles of both species increased. Recruitment patterns varied according to individual taxa, with extensive ontogenetic migration evident between mangroves and seagrass.

The data obtained are discussed in terms of application to the conservation and sustainable use of the mangroves as a habitat for the early life history stages of coral reef fish.

Glossary

Benthic	Associated with the bed of aquatic ecosystems
Demersal	Living on the bed of aquatic ecosystems
Detritus	Particulate material that enters into an aquatic system
Diel	Pertaining to the day – night cycle
Diurnal	Active during the day
Juvenile	Sexually immature fish with meristic characteristics corresponding to a mature adult
Larva	Stage of development between hatching and attainment of adult fin ray complement
Meristic characters	Enumerable morphological features
Nocturnal	Active during the night
Ontogenetic	Occurring during the course of an organism's development
Pelagic	Oceanic, relating to open water
Recruitment	The entry into a population of new individuals that have survived to a specified size after their settlement, without already being adult, or addition to successive life-cycle stages within populations
Settlement	The process of becoming associated with a habitat; influenced by habitat availability and selection
Spatial variation	Variability over a geographic area
Temporal variation	Variability on an hourly, daily or seasonal basis
Viviparous	Bearing live offspring

Apogon sp. larva

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1.0 Introduction

1.1. *Research rationale*

Many studies on shallow tropical marine ecosystems have shown that mangroves and seagrass beds are potentially important habitats for the early life stages of coral reef fishes (Robertson & Duke, 1987; Baelde, 1990). The importance of these nursery habitats is generally explained in terms of food and shelter availability, and predation pressure. This may be elucidated by a number of hypotheses:

(I) the availability of food is greater in mangrove stands and seagrass beds than unvegetated coastal areas or coral reefs (Odum & Heald, 1972; Ogden & Gladfelter, 1983);

(II) shelter against predators and photodamage is provided by the structural complexity of mangrove roots and seagrass blades, shade from overhanging vegetation, and high levels of turbidity (Helfman, 1981; Robertson & Blaber, 1992; Morgan & Christy, 1996);

(III) nursery habitats usually contain lower numbers of piscivorous predators (Shulman, 1984; Parrish, 1989).

The function of these habitats as nursery grounds is not always apparent, however, and remains unevaluated in many regions (Dennis, 1992; Nagelkerken *et al.*, 2000b). The mangrove habitat in particular is being lost at a rapid pace through deforestation, aquaculture and overexploitation of wood and fisheries resources, and current levels of use are unlikely to abate in the near future. As the pressure from population growth and development increases, a better understanding of mangrove ecosystem function is required in order to facilitate informed management decisions.

In order to formulate specific research questions to test the above hypotheses, consideration of the ecology of the mangrove habitat, its resident fish population, and their contemporary status in the selected study area of Belize, Central America, is required.

1.2. *The present and future status of the mangrove habitat*

Mangroves constitute woody halophyte-dominated ecosystems situated at the land-sea boundary. Most mangrove forests are highly productive, helping to support coastal food chains, including commercially valuable fish, crustaceans and molluscs (Figure 1.1). The world's mangrove forests are economically very valuable, worth an estimated US$ 180,895,923,000 (Costanza *et al.*, 1998). Situated in the tropics and subtropics, they are less species-rich than other tropical forests, with 9 orders, 20 families, 27 genera and roughly 70 species of mangroves occupying a total estimated area of 181,000 km^2 (Spalding *et al.*, 1997). Approximately 43 % of the world's mangrove forests are found in Indonesia, Australia, Brazil and Nigeria, with the most diverse biogeographical regions in the Indo-West Pacific.

The standing crop of mangrove forests is generally greater than any other aquatic ecosystem, with a decline in aboveground biomass with increasing latitude. They are structurally and functionally unique due to distinctive morphological and ecophysiological characteristics and adaptations such as aerial roots, viviparous embryos, tidal dispersal of propagules, rapid rates of canopy production, highly efficient nutrient retention mechanisms, salt tolerance and the ability to maintain water and carbon balance (Lugo & Snedaker, 1974; Twilley *et al.*, 1986).

Although mangroves offer few direct anthropogenic uses, they have been heavily used for tannin, timber, charcoal, food and medicines (Lugo & Snedaker, 1974; Adegbehin & Nwaigbo, 1990; Komiyama *et al.*, 1992; Smith & Berkes, 1993; Ellison & Farnsworth, 1996).

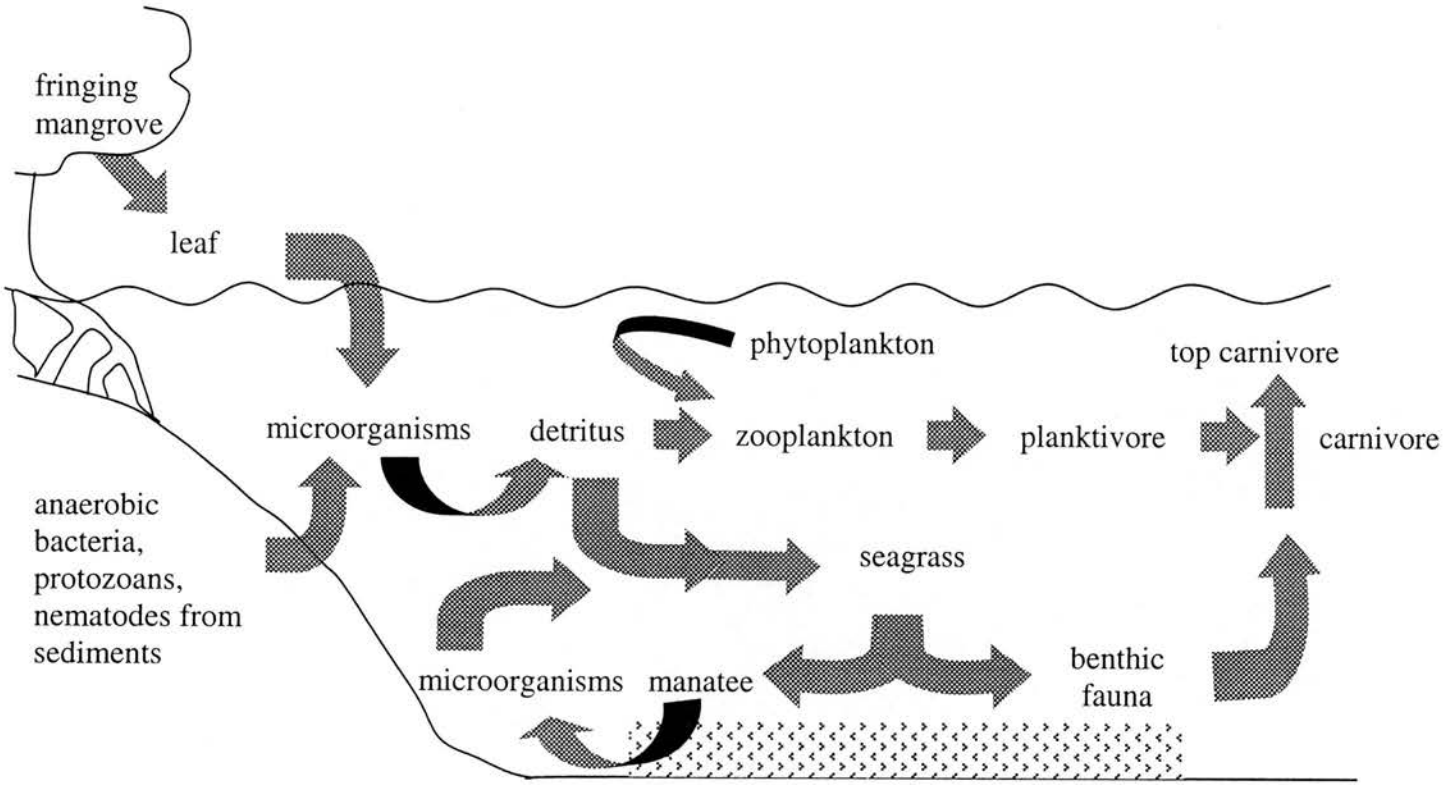


Figure 1.1. A simplified diagram of the detrital food-web in a mangrove-fringed estuary (adapted from Whitfield, 1999).

A long history of biological research on mangrove structure, productivity and ecosystem dynamics has led to a broad recognition of the biotic and socioeconomic services of mangroves (Farnsworth & Ellison, 1997). However, anthropogenic pressures are reducing the global range of mangrove forests and the current levels at which this habitat is exploited are unlikely to abate in the near future (Alongi, 2002). Many past and current abuses are now irreversible.

The greatest present-day threats come from the over-exploitation of wood and fisheries resources, and continuing deforestation for aquaculture and the development of coastal settlements (Pons & Fiselier, 1991; McShane, 1996). Aquaculture also affects surrounding ecosystems through the accumulation of waste, antibiotics and chemicals (Folke & Kautsky, 1992). Global production of farmed fish and shellfish in the coastal zone has more than doubled in the past 15 years (Naylor *et al.*, 2000). Despite this, aquaculture production in countries with mangroves appears to have levelled off, possibly indicating that a sustainable level has been reached and that mangrove clearing for aquaculture operations has peaked (Alongi, 2002). However, it remains a significant threat and there is a continued need for more space as aquaculture production per unit area is declining (Naylor *et al.*, 2000; FAO, 2001).

Deforestation is a major threat to the survival of mangroves. Although reforestation programmes continue and are likely to increase in future, the biodiversity lost, especially from old-growth forests, is unlikely to be regained for several decades, and perhaps permanently lost if species become locally extinct due to excessive fragmentation of habitats (Kaly & Jones, 1998; Al-Khayat & Jones, 1999). Coastal development for housing and industry also leads to eutrophication, from increased boat traffic and other uses of coastal waterways. These threats will in turn increase pressure for further development, and alteration of waterways.

Anthropogenic pressures on the mangrove ecosystem may be exacerbated by natural processes, such as climate change. The combustion of fossil fuels combined with deforestation and other forms of land clearing are leading to an inevitable rise in atmospheric CO_2 concentrations and temperatures, giving rise in turn to an increase in sea level as polar ice melts (IPCC, 2001).

In the next 20 years the atmospheric concentration of CO_2 is expected to rise by approximately 40 ppm from the 2000 average of 370 ppm to 410 ppm, temperatures may rise by 0.5–0.9°C, and sea level by 3–12 cm (IPCC, 2001). Although experimental evidence indicates that the responses of mangrove species may be complex, it also indicates that overall changes may not be significant (Semenuik, 1994; UNEP, 1994; Ball *et al.*, 1997). The expected rise in temperature may result in expanded latitudinal limits for some species, alteration of community composition, and marginal increases in photosynthesis, respiration, litter fall, microbial decomposition, floral and faunal diversity, growth and reproduction, but reduced rates of sediment accretion (UNEP, 1994). However, temperature changes in the tropics may not be as great as at higher latitudes (IPCC, 2001), and seasonality may be reduced due to changes in precipitation, which is likely to vary greatly on local and regional scales (UNEP, 1994).

The presumed rise in sea level is difficult to evaluate owing to past and recent variations in local relative sea level (Woodroffe, 1990; Rull *et al.*, 1999). Mangroves may progress landwards at a rate determined by the extent of sea level rise, the level of vertical accretion, and slope and space at the landward edge. Zonal patterns of plants and animals will be altered slightly and erosion at the seaward front will increase (UNEP, 1994). The ability of mangroves to accommodate future sea-level rise will depend on factors such as tidal range, sediment supply and tree species composition. These factors are likely to be magnified on islands, and in the arid tropics where rates of sediment supply,

available upland space and mangrove growth rates are usually low (Ellison & Stoddart, 1991; Parkinson *et al.*, 1994; Semeniuk, 1994).

To make realistic predictions for the future of mangroves, an assessment of the accuracy of the present losses and gains in forest area is required. While large tracts of mangroves have been severely degraded or destroyed worldwide, most data reflect inaccurate surveys, unsubstantiated claims or old estimates not based on empirical measurements (Farnsworth & Ellison, 1997; Burke *et al.*, 2001; Alongi, 2002). For example, in Fiji total mangrove area has been reported as between 19,700 and 49,777 ha (Spalding *et al.*, 1997). Long-term changes in mangrove area show that most countries have lost mangroves, especially Vietnam, Mexico, Singapore, the Philippines and Thailand. In Singapore, the losses were incurred over nearly a century, mainly as a result of urbanization (Hilton & Manning, 1995; Spalding *et al.*, 1997). Elsewhere, losses have been sustained mostly over the past 20–30 years as a result of clearing for aquaculture, urbanization and timber products. Vietnam's losses were sustained chiefly as a result of defoliation in the 1960s and early 1970s (Hong & San, 1993). Some countries, such as Papua New Guinea, Australia and Belize show no substantial change and a few, such as Cuba, have regained mangrove forests due to restoration projects (Field, 2000).

Although some publications cite a global loss figure of 50 %, approximately one-third of mangrove forests appear to have been lost over the past 50 years (Clough, 1993; Diop, 1993; Lacerda, 1993 Spalding *et al.*, 1997; Burke *et al.* 2001; Alongi, 2002). Spalding *et al.* (1997) found numerous inaccuracies in previous works because of what was considered mangrove forest. Future global changes in forest area are difficult to predict as loss rates vary greatly, ranging from 1 to 20 % of total forest area per year (Clough, 1993; Diop, 1993; Lacerda, 1993).

The fate of the mangrove habitat is intimately linked to changes in forest use, which is directly tied to changes in human population growth and development. Predictions of human population change indicate rapid growth in tropical developing nations, where the bulk of mangrove forests lie (Saha, 1995; Alongi, 2002). Assuming that human populations will grow along tropical coasts, so will anthropogenic impacts. Some mangrove areas are already overfished. For example, in the Mekong delta, fish catch per unit effort has been declining since the late 1970s, as the coastal population grows and mangroves continue to be destroyed for shrimp farming, which has increased 35-fold (de Graaf & Xuan, 1998). One hectare of mangrove presently supports approximately 0.45 tonnes of marine fish catch per year in the region. Increasing human pressures bring a rise in the incidence of viral and other diseases, directly impacting shrimp seed stock, as well as increasing coastal erosion and saltwater intrusion into groundwater (Hong & San, 1993; de Graaf & Xuan, 1998).

If mangrove resources are to be conserved, sustainable management must operate realistically, on the basis of economics (Turner *et al.*, 1993; Barbier, 2000). Case studies indicate that the idea of conserving mangroves as economic investment is realistic (Ronnback, 1999; Ronnback & Primavera, 2000). The mean monetary value of mangroves has recently been estimated at US$ 9990 ha^{-1} yr^{-1}, second only to the value of estuaries and seagrass beds, and greater than the economic value of coral reefs, continental shelves and the open sea (Costanza *et al.*, 1998). The commercial value of mangrove resources has been recognized since early last century. Mangrove-related fisheries resources are generally more valued than natural and agricultural goods, such as wood, with the value of fisheries ranging from US$ 120–3000 ha^{-1} yr^{-1} and timber from US$ 60–800 ha^{-1} yr^{-1} (Clough, 1993; Diop, 1993; Lacerda, 1993).

The competing demands of coastal industries and mangroves are manageable if relevant ecological information is collected and used properly to design management plans that reflect how mangrove ecosystems support fisheries. For example, until the mid-1980s, mangroves were heavily exploited in Colombia for artisanal and commercial fishing, wood extraction for poles, charcoal, paper and housing materials, with no clear national or regional plans for sustainable development (Lacerda, 1993). As a result of these unsustainable losses, the National Institute for Renewable Resources and Environment started a National Mangrove Committee with the aim to formulate policies for the conservation and sustainable management of mangroves in Colombia. As a result of these policies, mangrove protective areas have been enlarged and the coastline divided into areas for protection, public interest, forestry and fisheries reserve, special management and special protection (Lacerda, 1993). On the Caribbean coast of Colombia where semi-intensive shrimp aquaculture is practised, proper environmental management plans have been drawn up as a result of an urgent need for ecologically sustainable development (Larsson *et al.*, 1994).

Establishing a clear ecological and economic link between mangroves and the value of fisheries is not an easy task (Turner, 1992; Barbier, 2000). In the Philippines, felling of mangroves for aquaculture has been banned since 1981, but the continuing decline in fish catch per unit effort has increased pressure to re-examine the protective legislation. Janssen and Padilla (1999) compare the costs and benefits of mangrove conservation with those generated by various alternative plans of aquaculture and forestry. A comparison of net annual benefits of goods and services provided by mangroves indicates that aquaculture generates the greatest value at US$ 6793 ha^{-1} yr^{-1}, followed by forestry (US$ 150 ha^{-1} yr^{-1}) and fisheries (US$ 60 ha^{-1} yr^{-1}). However, Janssen and Padilla (1999) question whether it is possible to

adequately value the impact of losses of species and ecosystems on the way of life of the indigenous people.

Several studies modelling the trade-off between mangroves and resource use argue for minimal destruction or use of forests and associated waterways, especially against the backdrop of overfishing (Barbier, 2000). Barbier and Strand (1998) estimate the impact of change in mangrove area on nearshore shrimp production in Campeche, Mexico, using an open-access fishery model. Simulating a marginal decline in mangrove forest area, their model indicates an accompanying decline in shrimp harvest and an increase in price per kg harvest and cost per vessel. However, their model suggests that the fishery is sensitive to the level of mangrove exploitation, with a modest decline in mangrove area leading to a disproportionate decline in shrimp harvest and revenue if the ecosystem is deforested beyond current levels of 2 km^2 yr^{-1}. In addition, while mangrove deforestation contributed to a decline in the fishery so did the pervasive problem of overexploitation. Shrimp fisheries have probably been operating at or above sustainable limits, and better management and involvement of the community in controlling overfishing is therefore as critical as limiting the destruction of mangrove areas (Bailey, 1988; Grasso, 1998).

The ecological ties between mangroves and adjacent environments can serve as a key for sustainable management (Pons & Fiselier, 1991; Saha, 1995). Resource-use models encompassing the strength of linkages between ecosystem compartments show that severe restrictions on mangrove clearing can optimize economic output. In the Bintuni Bay area of Indonesia where mangroves are heavily exploited for woodchips, and artisanal and commercial fisheries, strong economic arguments exist for limited clearing (Ruitenbeek, 1994). Cost-benefit analysis of forest management options incorporating links among fishery production, mangrove use and clearance rates, erosion

control and biodiversity indicate that clear-felling of mangroves is a viable management option only when all the linkages are ignored (Ruitenbeek, 1994). Assuming that clear linkages exist between mangroves and environmental functions and fisheries, a ban on cutting is the optimal strategy, whereas if the linkages incorporate time lags on the order of years, selective cutting of 25 % of total harvestable mangroves is optimal (Ruitenbeek, 1994). In general, conservative cutting appears to be a good strategy, as a management decision based on minimal information is likely to be wrong, with severe long-term economic and ecological consequences.

Mangrove forests are less diverse than most other tropical ecosystems, and a significant problem in the future will be the loss of biodiversity. The prediction of mangrove responses to human impacts is difficult due to the lack of long-term data, and difficulty in distinguishing natural change from anthropogenic impacts. Despite a long history of research interest, there remains a lack of knowledge of many aspects of the mangrove habitat, such as its biochemistry, physiology, colonization processes and species diversity of flora and fauna (Rollet, 1981; Alongi, 2002).

Actions can be taken to improve conservation of mangroves, such as the adoption of international environment agreements and the development of controlled management systems (Pons & Fiselier, 1991; Folke & Kautsky, 1992; Smith & Berkes, 1993; Field, 1995; Ellison & Farnsworth, 1996). If mangrove forests are not seen as a fundamental economic and ecological resource to be treasured, they will continue to be exploited at current rates for the foreseeable future.

1.3. *The ecology of fishes*

The life cycle of coral reef fish consists of 5 main stages, which are the egg, yolk sac larva, larva, juvenile and adult. In tropical waters, reproduction may be more or less continuous but with peaks of reproductive activity tied to other environmental events, such as

rainfall (Munro *et al.*, 1973; Johannes, 1978). Early life stages may therefore be present throughout the year, but in differing abundances (Carter & Perrine, 1994; Lalli & Parsons, 1997). All the early life history stages are susceptible to several sources of mortality, and the larval stage in particular is highly vulnerable (Figure 1.2). The majority of reef fish produce pelagic larvae that have to colonize a benthic habitat in order to complete their life cycle (Richards & Lindeman, 1987; Doherty & Williams, 1988). The addition of individuals to local populations, following settlement from the pelagic larval phase to the benthic or demersal early juvenile phase, is referred to as recruitment.

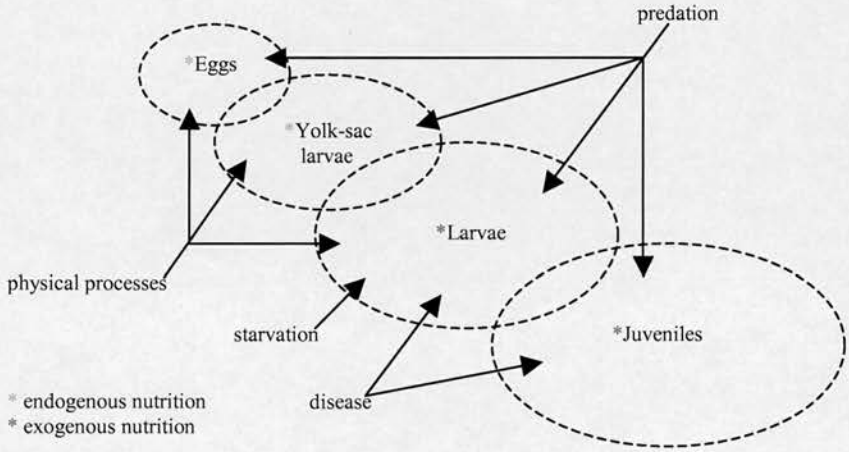


Figure 1.2. Diagrammatic representation of the major sources of mortality in the early life history stages of marine fish (from Houde, 1987).

Many species of fish are known to spend their different life stages in different habitats and even different geographic areas, perhaps migrating for 100s or 1000s of miles. Adult fish of many species migrate to spawning grounds far away from their home ground, with the result that the larval and juvenile populations do not always reflect the local adult population (Heath, 1992). While spawning grounds are often well known, in particular by fishermen, the dispersion of fish larvae and eggs, and the subsequent recruitment of juveniles, remains a topic of extensive scientific research.

The supply and recruitment of larvae are both considered to be determining factors in the structure of adult fish populations (Heath, 1992; Caley *et al.*, 1996; Holbrook *et al.*, 2000; Fraschetti *et al.*, 2003). Most local populations of marine organisms are deemed to be demographically open, with local recruitment uncoupled from local reproduction due to the dispersive larval phase. However, self-recruiting larvae may constitute a substantial proportion of the settling cohort (Jones *et al.*, 1999; Swearer *et al.*, 1999). In addition, the structure and dynamics of communities of marine species are often dependent on the interactions of a suite of biotic and abiotic processes that affect both recruitment and post-recruitment survival.

Physical transport processes, such as tidal currents or wind-induced surface currents, partly determine settlement distribution (Heath, 1992; Wolanski & Sarsenski, 1997). However, larvae appear to possess substantial sensory and locomotory capabilities that enable them to actively modify their dispersal patterns (Heath, 1992; Cowen & Sponaugle, 1997; Stobutzki & Bellwood, 1997; Fisher & Bellwood, 2000, 2002; Fisher *et al.*, 2000; Leis & Carson-Ewart, 1999; Armsworth *et al.*, 2001). Vertical orientation in the water column enables larvae to control their direction of travel, by maximising the effect of tidal currents or wind-induced surface currents, and some species are competent swimmers capable of overcoming background currents.

Spatial separation of size-classes between different habitats suggests movement from one habitat to another during life-cycle stages, and such migration has been inferred for many fish species, with larger individuals found progressively offshore (Yàñez-Arancibia *et al.*, 1988; Cocheret de la Morinière, 2002). Much of the reputation of specific habitats as important nursery sites comes from the presence of pre-recruits (i.e. larval or early juvenile stages), the adult stages often being found in different habitats. Such populations, which have survived the

highly vulnerable egg and yolk sac phases of early life, are often used as an indicator of adult populations, and fluctuations are generally associated with a reduction in spawning biomass. In order to validate this assumption it is necessary to assess the extent to which variation in the size of populations is due to variation in the influx of young or recruiting organisms.

Fish migrate between adjacent shallow water habitats due to feeding, spawning or ontogenetic behaviour, and so provide links between spatially separated communities (Figure 1.3). The timing of ontogenetic migrations are related to changes during the life-cycle of the fish, such as gradients or seasonal changes in environmental factors, physiological or morphological changes in juveniles, changes in diet or food distribution, and outgrowing the structural complexity of a habitat. Juveniles in nursery habitats are considered to be spatially separated from adults, with subsequent migration from the nursery to habitats occupied by adults occurring over a specific size range. To alleviate size-related competition, individual species may use different migration patterns, and may show a strong association with a specific habitat type where two are in close association. Many studies focus on a single methodology and as a result a single life stage, for example by not distinguishing between adult and juvenile fishes. As a result, the extent to which young and adult stages of marine organisms depend on different shallow water habitats is not clearly understood. This is especially so in the case of oceanic islands, where the shallow water habitats generally have a lower turbidity and greater circulation than mainland coasts (Dennis, 1992).

Predation and starvation are regarded as two of the most important processes in the survival of marine fauna, and are often used to explain the nursery role of habitats (Lasker, 1987; Young & Chia, 1987; Levin *et al.*, 1997; Baran & Hambrey, 1998). Predation is a key mechanism

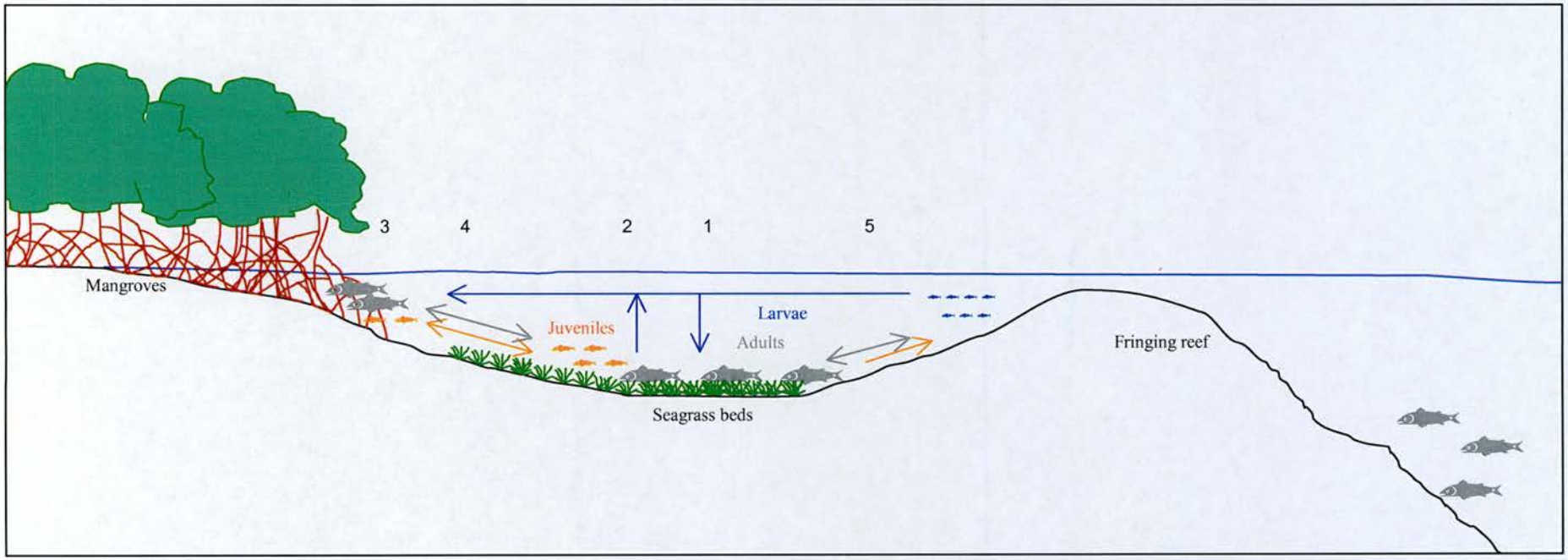


Figure 1.3 Ontogenetic migration patterns of the larval, juvenile and adult life history stages of reef fish species, between the fringing reef, seagrass beds and mangroves of a coral reef atoll. Fish larvae carried into the atoll lagoon from the reef may either settle into the seagrass or be carried over the seagrass beds into the mangroves (1). The seagrass larval assemblage may be augmented by spawning in the seagrass itself, and larvae may consequently be removed from the seagrass to the mangroves (2). The mangrove larval assemblage may also be supplemented by spawning within the mangrove habitat (3). In both the mangrove and seagrass habitat, larvae develop into juveniles, which either remain in the same habitat, migrate between the two habitats (4) or migrate to the coral reef (5). Adult fish either remain in a single habitat, or migrate between 2 or all 3 of the habitats (4, 5).

in structuring and maintaining diversity and stability in aquatic communities, as one of the effects on prey populations is intraspecific partitioning of resources, such as food and space (Stein, 1977; Drenner *et al.*, 1982; Frank, 1988; Öhman *et al.*, 1998). At community and population scales, prey selection by predators alters habitat selection behaviours and the life histories of prey species (Orth *et al.*, 1984; Kitchell *et al.*, 1994). Predators are size-selective, and therefore predation also impacts on the abundance and size distributions of prey (Brooks & Dodson, 1965; Hughes, 1997). If the density of a population is high enough for intraspecific competition to occur, the effects of predation on that population may be partly compensated for by a resulting reduction in intraspecific competition.

Planktonic invertebrates, such as copepods, and the larval stages of carnivorous fish, such as snappers, may have a significant role both as prey of planktivorous fish larvae and as predators, the former being known to consume fish larvae during the yolk-sac stage (Hunter, 1981; King, 1996; Dittel *et al.*, 1997; Bullard *et al.*, 1999; Whitfield, 1999). Adult planktivores, such as gobies, and the juvenile stages of carnivores also pose a risk (Brewer *et al.*, 1995; Greenfield & Thomerson, 1997). Predation is also a major cause of mortality for juvenile fish, both by adult piscivores and other juveniles (Carr & Hixon, 1995; Connell, 2000). The predation of larval and juvenile fish has consequent effects on their own prey, possibly to an extent that alters community structure and nutrient cycling at the whole ecosystem scale.

As predation is a major cause of mortality for the pre-adult stages of fishes, it is not surprising that mechanisms to minimise predation appear to play a significant role in their early life history. Predators may use active visual or static ambush tactics to capture prey (Hart, 1997). Active visual tactics involve actively searching out prey, and are therefore hindered by conditions that impede the vision of

predators, such as turbidity or complex habitat structure. When such conditions prevail, visual predators may switch to ambush tactics, in which case they wait for prey to come near them before attacking and capturing.

Prey species can minimise the risk from predators through predator avoidance or deterrence. A major predator-avoidance mechanism is the selection of habitats in which encountering predators is minimised, either due to extensive cover or low predator distribution (Kramer *et al.*, 1997; Smith, 1997). Such habitat selection may take the form of diel movements either vertically within the water column or between habitats (Wurtsbaugh & Li, 1985; Ryer & Olla, 1998; Clark *et al.*, 2003). A major predator-deterrence mechanism of fish is aggregation into schools or shoals. The grouping of prey together in schools or shoals decreases the risk of capture, even though the level of predation would be expected to increase with prey density (Cushing & Harden, 1968; Taylor, 1976). Aggregation formation appears to be a more important anti-predator process during daylight than at night, indicating that the main risk is from visual predators (Ryer & Olla, 1998).

The anti-predator benefits of any defensive mechanism to larval and juvenile fishes must by balanced against its effects on feeding. Therefore habitats that offer optimal protection against predators may not be utilised if the benefit of low predation risk is out-weighed by the disadvantages of poor nutrition. This may be overcome by variation in diet, either at different life stages or within a single life stage (Pollard, 1984). In addition to predation or starvation risks, habitat selection by fishes may be further influenced by physical or chemical characteristics of the water column, and in the natural environment their distribution may be determined by interaction between all four.

1.4. *The role of mangroves as a habitat for fishes*

Numerous studies of mangroves indicate their importance as a habitat for marine fauna communities, with habitat loss resulting in a lowering of population densities and loss of diversity of most mangrove-associated organisms (Heald & Odum, 1970; Ambak & Harmin, 1982; Hatcher *et al.*, 1989; Robertson & Blaber, 1992; Baran & Hambrey, 1998). However, the biological importance of mangroves in terms of fisheries yield is not normally reflected in ecosystem-level budgets (Barbier, 2000). The relationship of fish landings to mangrove data differs between regions owing to differences in catch methods, structure and productivity of forests, as well as the fisheries species in question (Chong & Sasekumar, 1994). The human impact on fishery yields in mangrove-dominated regions is not doubted, however. In southeast Asia, the growth of the trawl fishing industry has led to overfishing, habitat destruction and environmental stress in many areas (Mohsin & Ambak, 1996; Hinrichsen, 1998).

Fish in mangrove habitats may be divided into two broad behavioural types: true residents, which spend their whole lifecycle in mangroves, and partial residents, which are associated with mangroves in the larval and juvenile stages, or as adults (Boonruang & Janekarn, 1986; Kimani *et al.*, 1996). Temporary residents may be tidal or seasonal visitors, and high densities of transient partial residents may be maintained in mangroves for several months (Bell *et al.*, 1984). Marine fauna that spend phases of their early life in the mangroves vary as to whether they spawn in or outside the mangroves. If spawning outside the mangrove system, fauna may enter the mangroves either as larvae or as juveniles, the latter following completion of the larval phase offshore (Staples, 1980a, 1980b; Primavera, 1991; Whitfield, 1999). They may leave the mangroves while still in the juvenile phase, or may remain until they have attained adulthood.

Many coastal species spend critical early stages of their lives in mangrove waters, and densities of juvenile fish in mangrove estuaries are high compared with other estuarine habitats (Robertson & Duke, 1987; Whitfield, 1999). They are generally accepted as important nursery grounds despite statistical arguments to the contrary, and the difficulty in assessing their role, especially in relation to adjacent habitats such as seagrass beds, which often seem equally important for early life stages of fauna (Robertson & Duke, 1987, 1990; Hatcher *et al.*, 1989; Dennis, 1992; Sheridan, 1992; Baran, 1999). In the Caribbean, the function of seagrass beds and mangroves as nursery habitats for reef fish has been generally accepted, although quantitative data on ontogenetic shifts in habitat use from nursery to adult habitat association are largely lacking and the relative importance of nurseries to different size-classes of reef fish species is poorly known (Parrish, 1989; Rooker & Dennis, 1991; Sedberry & Carter, 1993; Nagelkerken *et al.*, 2000). The benefits of mangroves to the early life stages of reef fish is generally discussed in terms of high food availability, high interception rate of vegetation to planktonic larvae, shelter against predators and low predator abundance (Odum & Heald, 1972; Blaber & Blaber, 1980; Orth *et al.*, 1984; Parrish, 1989; Robertson & Blaber, 1992; Baran & Hambrey, 1998; Nagelkerken, 2000).

Very few fish species have been identified as obligate users of mangroves and most are assumed to have a facultative mangrove dependency. The full relationship of fish with the mangrove habitat can only be accurately assessed through analysis of all three life stages in the same geographical area. When considered with the habitat structure, the most probable selective pressures, i.e. availability of food or shelter, or level of predation, may be better understood and so the level of dependency of individual species on their habitat.

In Caribbean mangrove forests leaf litter is processed primarily via the detrital pathway, and detritus has long been regarded as an important

source of organic carbon and nitrogen in the diets of the early life stages of fish and invertebrates (Odum & Heald, 1972; Heald *et al.*, 1974; Lugo & Snedaker, 1974; Odum & Heald, 1975). Recent studies question the actual nutritional value of detritus and suggest that it is the microorganisms associated with detritus, such as bacteria, which are an important food source (Boesch & Turner, 1984; Chong *et al.*, 1996; Dittel *et al.*, 1997; France, 1998). In addition, the early life-stages of marine organisms such as shrimp are often able to select specific prey items from the detritus and benthic fauna of the mangrove sediments (Moriarty & Barclay, 1981; Wassenberg & Hill, 1987; Dittel *et al.*, 1997). Thus the productivity of mangroves as expressed in terms of leaf litter is supplemented by the activity of benthic bacteria, diatoms and microalgae, as well as epiphytic algae fixed on mangrove roots (Rodriguez & Stoner, 1990; Rützler & Feller, 1996). Overall, this production allows the development of a dense zooplanktonic and benthic fauna (Alongi, 1990; Mitsch & Gosselink, 1993). Mangrove communities are not entirely detritus-driven, however, as evidenced by the larval, juvenile and adult stages of fish present in the mangrove system, the majority of which are planktivores (Houde & Schekter, 1980; Whitfield, 1999).

The role of protection against predation is mainly facilitated by the dense web of mangal pneumatophores and prop roots, where numerous post-larvae and juveniles can escape or hide from large and small predators (Robertson & Duke, 1987; Thayer *et al.*, 1987; Al-Khayat and Jones, 1999). Visual predators can see much further in structures of low complexity, while in highly complex habitats longer search periods are probably required and encounter rates are lower. However, the extent to which habitat structural complexity offers protection may be species specific, and it cannot be assumed that more dense habitats provide more protection (Macia *et al.*, 2003). Interaction may occur between habitat complexity, such as prop-root density, and other factors affecting predation, such as turbidity and prey density.

The fine sediment trapped by mangrove root systems often gives rise to elevated levels of turbidity, which aids in concealing larvae and juveniles from visual predators (Mitsch & Gosselink, 1993; Laroche *et al.*, 1997; Whitfield, 1999). However, its effect depends on the behaviour of both prey and predators, predominantly the former as the visual reactive distance of predators is reduced in turbid water (Moore & Moore, 1976). Nevertheless, some fish species that use visual cues are able to capture prey at very low light intensity, with some changing from active chasing to ambush type predation in very turbid conditions (Minello *et al.*, 1987; Macia *et al.*, 2003).

The shadow created by leaf cover is also thought to enhance survival of larval and juvenile fish, by reducing contrast and so reducing the distance from which predators can see their prey (Helfman, 1981). Overshadowing and increased turbidity may both lessen the need for diel vertical migration, a behavioural strategy used by many aquatic animals to avoid predation (Morgan & Christy, 1996). Both planktonic and nektonic organisms may rise to the surface at dusk to feed, and sink again at dawn (Dobson & Frid, 1998; Abello & Guerao, 1999). Reverse diel migrations are evident in some planktivorous and piscivorous species, which may remain at or near the water surface throughout the diel cycle (Ryer & Olla, 1998).

Attempts have been made to attribute general rules to mangroves, stating either that they are (Robertson & Duke, 1990; Wakwabi & Mees, 1999) or that they are not important as nursery sites (Robertson & Duke, 1987; Dennis, 1992; Sheridan, 1992). Often a mangrove system has been deemed important if pre-adult stages are considered to be solely dependent on it and not on other habitats. This follows Beckley's (1984) statement that juveniles may only be concluded to be dependent on a particular habitat if they are found to be absent or scarce in others. For example, some species of grunts (*Haemulon* spp.), barracuda (*Sphyraena* spp.) and snapper (*Lutjanus* spp.) are

described as distinctive of the mangrove habitat in their pre-adult stages, with young juveniles rarely seen in adjacent habitats (De Sylva, 1963; Thayer *et al.*, 1987; Dennis, 1992). All have a wide global distribution, and the life cycles of individual species have been studied in detail at local levels (De Sylva, 1963; Starck, 1971; Greenfield & Thomerson, 1997). However, knowledge of the life cycles of the majority of marine species remains limited, making it difficult to predict the distribution of different life stages between inshore and offshore habitats (Abello & Guerao, 1999; Moueza *et al.*, 1999).

Variation in biotic and abiotic factors on global and local scales poses problems when trying to apply general rules to the relationships between mangroves and marine fauna. The most fundamental of these are variations in the biogeography of mangrove species. Mangrove stands that differ in substrate and species may each have distinctive marine fauna (Blaber & Milton, 1990; Boulon, 1992; Al-Khayat & Jones, 1999). Zoogeographic patterns are a further factor to be considered. The fauna of the Indo-Pacific is much more diverse than that of the Atlantic, with more families, genera and species of mollusc, crustacean, echinoderm and fish, and a higher level of endemism (Illies, 1974; Lowe-McConnell, 1977). Within each of these two regions tropical and subtropical marine faunas are similar, and much more diverse than temperate fauna, with diversity increasing toward the equator (Longhurst & Pauly, 1987; Whitfield, 1999). The wide range of species diversity in mangroves which is recorded globally (e.g. Blaber *et al.*, 1985; Robertson & Duke; 1987; Blaber & Milton, 1990; Laroche *et al.*, 1997; Lorenz *et al.*, 1997; Al-Khayat & Jones, 1999) may be partly accounted for by zoogeographic variation (Little *et al.*, 1987; Whitfield, 1999), but this is seldom considered in the literature and is perhaps beyond the scope of most studies.

The number of microhabitats is a major factor influencing community composition of fish. However, the number of microhabitats in turn

relies on environmental factors such as water quality, salinity, temperature, tidal range and turbidity (Robertson & Blaber, 1992; Baran & Hambrey, 1998; Whitfield, 1999). Annual fluctuations of these can have significant negative and positive effects on marine fauna (Turner & Boesch, 1988; Ferraris *et al.*, 1994), and as most studies have been conducted over 1 or 2 years, an unusual event in a single year may make results less representative of long-term trends.

The structural complexity of the mangrove habitat may itself have an effect on abundance and diversity of marine species, but has proved difficult to measure and has been rarely investigated in detail (Skilleter, 1996; Baran & Hambrey, 1998; Beck, 1998; Whitfield, 1999). A more detailed understanding of how pre-adult life-stages utilize the mangroves is required. Once the significance of the role played by this ecosystem is established, the consequences of its loss or modification may be better understood. It may also add to the present knowledge of the life cycles of marine fauna. Although the life cycles of some fauna have been investigated in detail, there remains a paucity of information, in particular for tropical taxa (Doherty & Williams, 1988; Abello & Guerao, 1999; Moueza *et al.*, 1999; Whitfield, 1999). Early life-stages are often described to provide basic knowledge for aquaculture, and descriptions may not cover every stage in an organism's development.

1.5. *Methods of investigating fish populations*

Investigations involving the larvae and eggs of marine fauna have frequently been used in attempts to understand and solve fisheries problems, through assessment of the species identification and distribution, biomass, recruitment and production of a fishery (Smith & Richardson, 1977; Lasker, 1987; Baran & Hambrey, 1998). Although studies have found positive correlations between mangrove area and fishery catches, many call for further research to validate the connection between the two (Turner & Boesch, 1988; Dennis, 1992; Primavera, 1997).

The complex bathymetry and spatial heterogeneity of tropical inshore habitats provides inherent sampling problems for fisheries ecologists and often limits the use of conventional sampling methods. In addition, larval fish are exceptionally difficult to study in the field. They are generally rare in the water compared to zooplankton organisms of equivalent body size, and extremely agile and proficient at evading nets or other towed devices. They are fragile and highly vulnerable to damage by physical contact, and there is no alternative to positive identification by eye of individuals down to species, making sample processing highly time-consuming. The use of light-aggregation devices is an alternative collection method that has been developed to sample larval fishes in complex habitats (Gregory & Powles, 1988; Choat *et al.*, 1993; Brogan, 1994). Light traps may compensate for stratification when it is present, as conventional trap designs sample a range of depth strata simultaneously by design of their illumination (Fisher & Bellwood, 2002). Light-aggregation devices use a light at night to aggregate larval fishes for capture, which are then collected by pumps (Bullis & Roithmayr, 1971), nets (Rooker *et al.*, 1996) or traps (Brogan, 1994). The evaluation of the effectiveness of light-aggregation devices is complicated by a wide range of trap designs, and differing methods of deployment.

Geographic variation in larval distributions produces inherent variability in the results of studies using similar methods. There is also inherent temporal variability, as demonstrated by comparison of 3 studies conducted in different years at the same site off Lizard Island, Australia, in which the mean number of fish larvae captured per light trap ranged from 1.5 to 4.9 to 190 individuals per hour respectively (Doherty, 1987; Choat *et al.*, 1993; Fisher & Bellwood, 2002). However, it appears that no studies have been conducted for longer than two consecutive years using identical light-aggregation methodology at the same site. Within year variability due to tidal

cycles and lunar phases has been detected in Caribbean and Indo-Pacific studies, with peaks in larval numbers generally occurring with the new and three-quarter moon (Thorrold *et al.*, 1994; Doherty *et al.*, 1994; Rooker *et al.*, 1996; Sponaugle & Cowen, 1996a, 1996b; Kingsford & Finn, 1997; Hickford & Schiel, 1999).

The collection of larval samples at night partly counteracts sampling problems due to the stratification of larvae, as this appears absent or reduced at night (Choat *et al.*, 1993). In addition, most larvae probably settle between dusk and dawn (Victor, 1991). Studies in which diel variation in larval distributions is evident have generally found much greater numbers present at night, although this may also be a result of reduced stratification (Thorrold *et al.*, 1994). Sampling duration has rarely been considered a source of variability, with most studies assuming that the abundance of larvae collected will be proportional to the period of light trap deployment. Rooker *et al.* (1996) found an optimal catch per unit effort (catch per minute) of 10 minutes, using a nightlight lift-net. However, the maximum sampling duration used in the study was 20 minutes, and the design of the collection apparatus was reliant on larvae remaining at the light source. By contrast, the majority of light trap designs consist of a light source enclosed in a large container with small openings, which retain captured larvae around the light (Gregory & Powles, 1988; Choat *et al.*, 1993; Brogan, 1994; Ponton, 1994; Sponaugle & Cowen, 1996a, 1996b; Hickford & Schiel, 1999; Röpke *et al.*, 1999; Meekan *et al.*, 2000; Watson *et al.*, 2002). Meekan *et al.* (2000) suggest that small entrances into light traps may decrease their efficiency due to the probability of fish encountering the openings, but simultaneously suggest that the same factor impedes escape.

Associated with the sampling duration at night is the time of night at which collections are made. Although several studies suggest this has no significant effect on the performance of light traps, no quantitative

analysis has been published to date to support such an assumption (Holmes & O'Connor, 1988; Watson *et al.*, 2002).

1.6. *The study site: Belize*

Belize has an area of 22,963 km^2 and is bordered by Mexico to the north, by Guatemala to the west and by the Caribbean Sea to the east (Figure 1.4). The Caribbean Sea is the second largest in the world with an area of 2,515,900 km^2. It is composed of four deep basins. The Venezuelan Basin in the east is partially separated from the Colombian Basin in the west, and both lie to the south of the Cayman Trough, which runs from north of Jamaica to Belize. To the north of the Cayman Trough lies the fourth, Yucatan Basin.

The continental shelf of Belize lies between 15°50'N and 17°55'N, and is narrow at 13-28 km, extending east from the mainland to a seaward boundary at a depth of 180 m. Five submarine ridges provide the supportive framework for a 600 km long reef system that lies offshore from Belize, which includes the second longest barrier reef in the world and three of the four oceanic atolls in the western hemisphere (Gischler & Hudson, 1998).

Along the coast of Belize, winds are steady from the northeast, east, and southeast at 3-8 ms^{-1} (Stoddart, 1962). Trade winds result in easterly winds for most of the year. With wind-generated currents more influential than tidal currents, there is generally a westward-flowing surface current with some upwelling along the South American continent. At the Gulf of Honduras in southern Belize, the main current is diverted north, creating a southward-flowing countercurrent (Gischler & Lomando, 1999). From October to January northerly winds and heavy rain are brought from continental North America,

Figure 1.4. Bathymetry of the Caribbean Sea and adjacent areas (based on http:// www.lib.utexas.edu; Richards, & Bohnsack, 1999).

with winds gusting up to 31 ms^{-1}. Belize is also affected by hurricanes moving through the western Caribbean, with strong easterly winds and high meteorological tides. The normal tidal range on the coast of Belize is 0.3 m but may reach 0.8 m during northers (Heyman & Kjerfve, 1999). The climate is sub-tropical with average air temperatures of 27°C in the summer and 24°C in the winter. Precipitation in the north of Belize ranges between 1240 and 1780 mm/year, and exceeds 3800 mm/year in the south, but on the atoll platforms it is much lower with an average of just 500 mm/year (Stoddart, 1962; Purdy *et al.*, 1975). Surface oceanic water temperatures range between 29 °C and 26 °C off the Belize coast (Garcia & Holtermann, 1997).

Beyond the barrier reef the shelf slope dips 40° into abyssal waters. There are two main hydrographic provinces: the barrier platform, which consists of the barrier reef, backreef lagoon, and cay complex, and the shelf lagoon, which at the latitude of Belize City consists of bathymetrically distinct sections north and south of the Belize River delta. The northern part of the shelf is bordered by a low karsted surface of flat-lying Cenozoic and Cretaceous carbonates with a few small rivers draining onto the shelf (James and Ginsburg, 1979). The inner shelf is generally flat, extending to a depth of only 8 m. The southern continental shelf is bordered by the Maya Mountains, through which many rivers flow onto the shelf. The depth of the shelf lagoon ranges from 25 m near Belize City to 200 m near Honduras (James and Ginsburg, 1979). The three atoll platforms are surrounded by deep water and have surface breaking reef rims (Figure 1.5). Depths between the atolls and the barrier reef range from 250 m to 400 m.

The wide, gently inclined continental margin does not benefit from upwelled nutrients, instead the primary source of nutrients is watershed runoff and the release of organic material from the degradation of intertidal and subtidal vegetation and coral reefs (Birkeland, 1990; Heyman & Kjerfve, 1999). Coupled with the presence of the barrier

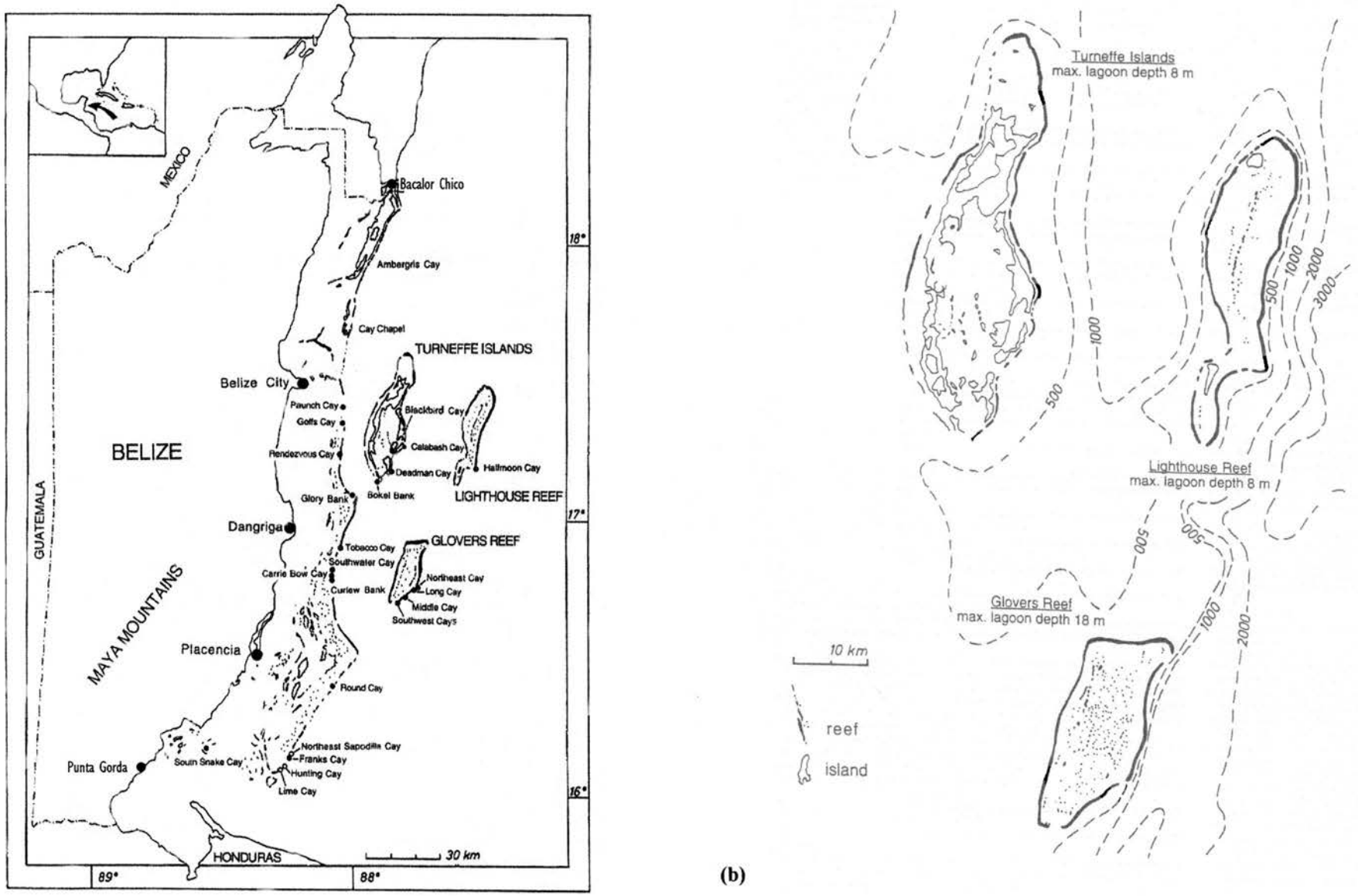


Figure 1.5. (a) Location of barrier reef and coral reef atolls off the coast of Belize (from Gishler & Lomondo, 1997). (b) Bathymetry of the three coral reef atolls, with depth contours in metres. Depths between Turneffe Islands and the barrier reef reach approximately 250 m (from Gischler & Hudson, 1998).

reef and the narrow tidal range, the coastline's shallow gradient has provided a sheltered environment for the development of extensive mangrove cover on the Belize coast and cays.

Covering 78,511 ha, Belize's mangrove stands consist of three true species: *Rhizophora mangle* L., *Avicennia germinans* (L.)L. and *Laguncularia racemosa* (L.) Gaertn.f. plus the mangrove associate *Conocarpus erectus* L. (McShane, 1996; Murray *et al.*, 2003).

1.7. *The status of mangroves and fisheries in Belize*

The present level of mangrove cover in Belize is estimated to be 98 % of original levels (Murray *et al.*, 2003), but clearance for development purposes is continuing in the absence of detailed knowledge of the importance of the mangroves. Although legislation is sufficient to conserve mangrove forests, inadequate resources and insufficient political will exist to enforce it (Zisman, 1998). Belize has ratified several international environmental agreements applicable to the conservation and management of mangroves: the Convention Concerning the Protection of the World Cultural and Natural Heritage, the Convention on International Trade in Endangered Species of Wild Fauna and Flora, the United Nations Convention on the Law of the Sea, and the Rio Convention on Biological Diversity. The main legislation for managing mangroves in Belize is the Forests (Protection of Mangroves) Regulations, effective since 1989. A permit from the Department of Forestry is required to cut mangroves and fines are levied for illegal clearance. In addition, the Ministry of Tourism and Environment co-operates with other public agencies that have interests in mangrove management, notably the Fisheries Department and the Ministry of Economic Development.

Other legislation with implications for mangrove management includes the National Parks Systems Act of 1981 and the Natural Resources and Wildlife Protection Act of 1981. While such legislation affords

protection to the mangrove habitat, land laws, such as the Crown Lands Ordinance, the Land Tax Act, and the Land Utilization Act, appear to discourage mangrove conservation. The Land Tax Act, for example, allows taxes to be levied on privately owned land, based on its unimproved value, which in effect provides an incentive to clear mangroves. The Belize City Council extended the city boundaries in 1991 on the basis of a zoning and development plan from the Belize City Housing and Planning Unit (McShane, 1996). The plan recommended the conservation of productive mangroves within the city limits and the maintenance of coastal and riverine mangrove buffer zones. However, mapping of the Belize City area in 1994 showed the clearance of 519 ha since 1992, a 0.7 % reduction in the national total (Murray *et al.*, 2003). At present the greatest threats to the mangrove habitats of Belize come from continuing deforestation for aquaculture and the development of coastal settlements, as well as the over-exploitation of wood and fisheries resources (McShane, 1996).

The mangrove habitat also receives limited protection from some of the extensive marine conservation in place in Belize, with nine regions protected as marine reserves, national parks or natural monuments, and two more marine reserves proposed. Increases in fishing and tourism are exerting continuous pressure on the marine ecosystems, the latter especially through construction and development. A large part of the growing tourism industry is catered towards scuba divers visiting the atolls and barrier reef, and 78 % of hotels are located in the coastal zone (Garcia & Holtermann, 1997).

Although tourism is now Belize's largest industry, primary agriculture, fisheries and forestry account for 29 % of employment and more than 21 % of the GDP of Belize. Fisheries alone contributed 7 % of the GDP in 2001. The fishing area of Belize consists of the EEZ covering 169,840 km^2 and a shelf area of 9,800 km^2. A complex system is formed by the barrier reef (the largest in the Atlantic Ocean at 220 m

length), the three offshore atolls (Lighthouse Reef, the Turneffe Islands and Glovers Reef), patch reefs, seagrass beds, several hundred cays of sand and mangrove, extensive mangrove forests, coastal lagoons and estuaries. The total area fished is estimated to be 4,700 km^2 within a depth range of 1.5 – 10 m^2. Fishing pressures are not well documented but are thought to be increasing (Garcia & Holtermann, 1997). In 2001 fish exports were valued at US$ 9 million, a decrease from 1995 estimates of US$ 10 million (Gibson *et al.*, 1995).

In general, it is accepted that global fisheries are in crisis, most having reached their sustainable limits and some having collapsed (Roberts, 1997b; NRC, 1999; Richards & Bohnsack, 1999; Stergiou, 2002; Myers, 2003). The major fishery in Belize and the rest of the Caribbean Sea is in shallow-water coralline reef areas, and is fundamentally artisanal. A long history of reef use exists in Belize, commencing with the Maya Indians between 300 B.C. and 900 A.D. (UNEP/IUCN, 1988).

Today fishermen number 3000 – 4000 in Belize, with approximately 60 % belonging to a system of fisheries cooperatives established in the 1960s. Some aquarium fish trade occurs in addition to food fish capture. As with the mangroves, there is a substantial level of fisheries regulation in place mainly designed to protect heavily exploited species. These include controls over the taking and trading of lobsters (*Panulirus argus*), conch (*Strombus gigas*), turtles, bonefish (*Albula vulpes*) and Nassau grouper (*Epinephelus striatus*), and closed fishing seasons during the spawning periods. However, as with mangrove legislation, insufficient resources exist to guarantee full monitoring of fisheries and enforcement of fishing regulations.

The effects of such regulation are very localised, however. Strong connectivity appears to exist between Belize and other areas of the Caribbean, with a substantial input of larval supply to Belize from the

Yucatan Basin and north of Cuba, and larval export from Belize along the Cayman Trough to Jamaica and southern Cuba (Roberts, 1997a). Management schemes protecting specific habitats or areas do not address the connectivity of such systems, and greater import may be needed on the possible consequences of continuing degradation of shallow water habitats and their fisheries. This in turn requires an increase in the knowledge and understanding of processes at a local scale.

1.8. *Research aims and thesis outline*

The overall aim of this thesis is to analyse the factors influencing the recruitment of coral reef fishes (food and shelter availability, and predation pressure) to a mangrove island within an atoll system. Central to the population management of many groups, such as fish, is the assumption of an underlying relationship between spawning biomass and subsequent recruitment. Such relationships are hard to demonstrate and define. The large variance in recruitment, which tends to obliterate any underlying stock-recruitment relationship, is often attributed to the effects of environmental variations on the survival of egg and larval stages. Thus it seems justified to aim to increase the understanding of the underlying processes affecting survival and so recruitment to a parent population. Central to this is establishing the spatial and temporal distributions of early life stages within the mangrove habitat and which factors are most influential in determining these distributions.

The reputation of mangroves as an important nursery site largely comes from the presence of pre-recruits (i.e. larval or early juvenile stages), the adult stages usually being found in different habitats. Such populations, which have survived the highly vulnerable egg and yolk-sac phases of early life, are often used as an indicator of adult populations, and fluctuations are generally associated with a reduction in spawning biomass. In order to validate this assumption it is necessary to assess whether variation in the size of populations is due

to variation in the influx of young or recruiting organisms. To do this the present study investigates how the patterns of larval supply to Calabash Cay vary on spatial and temporal scales and whether the patterns of larval supply correspond with the patterns of larval abundance in the mangroves.

The high structural complexity of the subtidal mangrove habitat in theory renders it very attractive to early life stages, which are vulnerable to predation. Although numerous studies support the hypothesis that coastal marine faunal resources are closely linked to mangroves, the degree of dependence remains controversial, not least because the ecological dependence of fauna on mangroves remains poorly quantified. There is therefore a need to establish whether the abundance and distribution of early life stages of marine fauna are functions of the complexity of their habitat structure. While this may be assumed through the presence of simple correlation between mangrove stand density and/or overshadowing, and pre-recruit abundance, it is difficult to separate out other contributing factors such as water depth or larval supply.

Small-scale studies may help to establish whether quantifiable relationships exist between physical attributes of mangroves, such as density and structural complexity, and pre-recruits. The most preferred habitat is not necessarily the one in which the greatest proportion of the population occurs. Many habitat features are correlated in nature, and so features that appear associated with preferential use may not necessarily be features selected by the fish. To establish whether the abundance of these stages is related to subsequent recruitment to the adult populations, the present study investigates whether there is a correlation between the patterns of larval abundance in the mangroves, and therefore larval supply, and the abundance of more developed juvenile stages.

To accurately assess the full relationship between fish and the mangrove habitat, analysis of all three life stages in the same geographical area is required. When considered with the habitat structure, the most probable selective pressures, i.e. availability of food or shelter, or level of predation, and so the level of dependency of individual species on their habitat, may be better understood.

The first step is to establish the taxonomic composition of the larval, juvenile and adult stages of fishes present in the shallow water habitats. To analyse the spatial distribution patterns, the following research questions may be addressed:

1. Do the larval, juvenile and adult life stages of reef fish display any preference for mangrove or seagrass habitats?
2. Within each habitat, are the density and size distribution of the larval, juvenile and adult assemblages influenced by variation in the habitat structure and other environmental variables?

Temporal patterns may be addressed with the questions:

1. How influential is the temporal variation in environmental factors on the temporal patterns of larval density and size distribution in the mangrove and seagrass habitats?
2. Is the density and size-distribution of larval supply stable across varying timescales of hours, days and weeks?
3. Does the taxonomic composition of larval supply exhibit variation over differing temporal scales?

The interaction of the three life-stages may be analysed by asking:

1. Is the larval supply related to the juvenile assemblage?
2. Is recruitment related to spawning (adult) stock in mangrove fish populations?
3. Do reef fish taxa display any preference for mangrove or seagrass habitats during the larval, juvenile and adult life stages?

The influence of factors other than habitat type may be addressed through the research questions:

1. How influential is the temporal variation in environmental variables on the assemblage composition of larval reef fish in the mangrove and seagrass habitats?
2. Is prey availability a more significant factor than shelter availability in habitat selection by (juvenile) reef fish?

In responding to the research questions, the appropriateness of the techniques used, the usefulness of the measures employed and the ability of a biogeographical viewpoint to provide useful information on fish population structure and diversity in two important shallow water habitats will be discussed. The overall thesis framework is outlined in Figure 1.6.

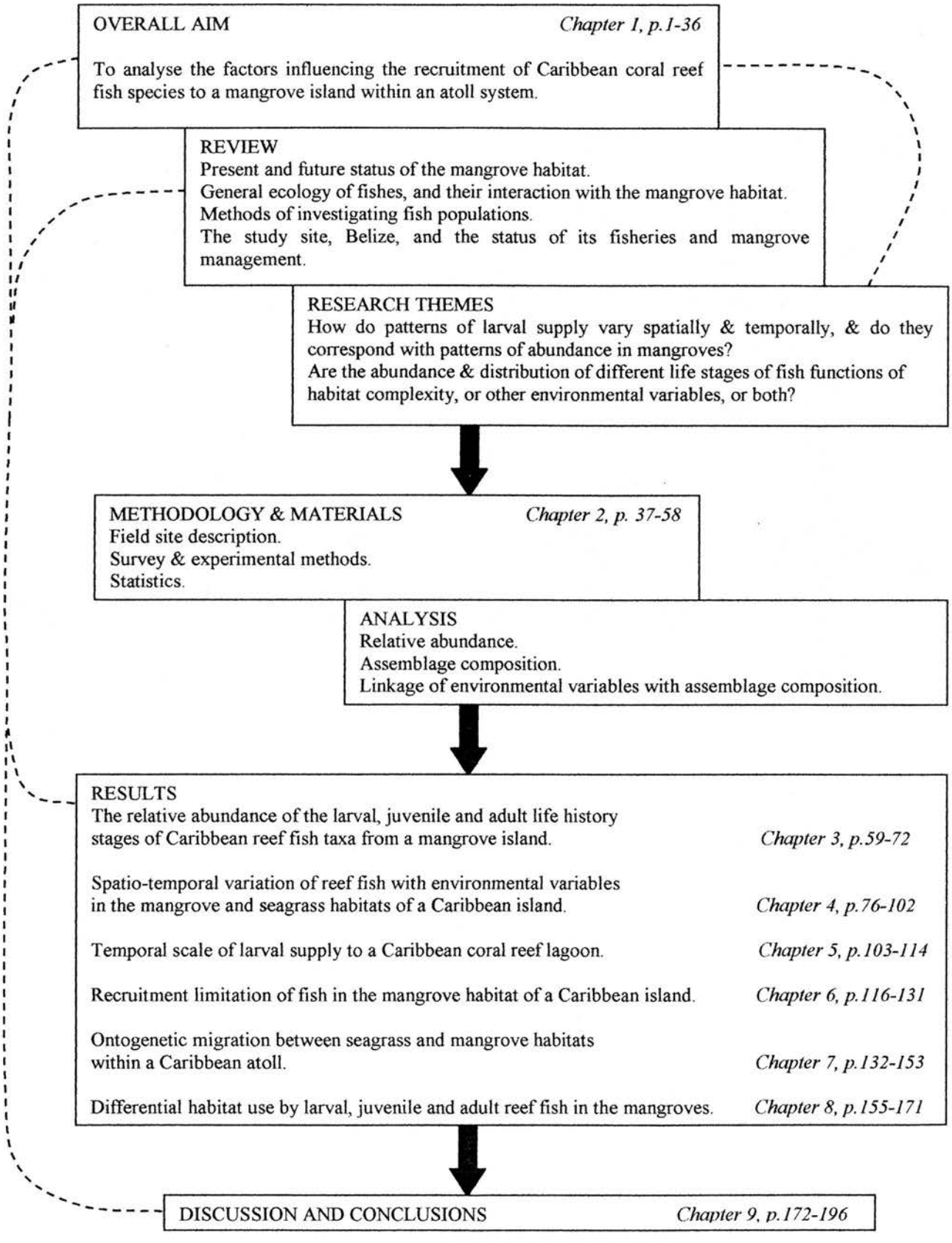


Figure 1.6. Thesis framework.

2.0 Materials and methodology

2.1. *The study area*

The country of Belize, in Central America (Figure 1.4), was selected to undertake the present study, due to a combination of historical, political and physical factors. Historically, members of the Department of Geography at the University of Edinburgh have conducted research in Belize for almost 40 years and a memorandum of understanding exists between the Department and the University of Belize (formerly the University College of Belize). The small size of the country (approximately 350 km long by 100 km wide), its relative political stability and the use of English as the official language give it logistical advantages over many other countries.

The population density is the lowest of all the Central American countries, and the proportion of protected land is the reported to be the greatest (over 35 per cent) in the northern hemisphere (Eltringham, 1999). As a result the pressure on the country's coast and extensive mangrove forests, which cover a total area of approximately 730 km^2, is limited. Nature exerts its own pressures, however, and the months of September, October, November and December are generally regarded as the hurricane season, when tropical storms frequently occur, and occasionally hurricanes. Hurricane Hattie caused extensive devastation in 1961 (Stoddart, 1972). More recent hurricanes have been relatively less severe but have still caused substantial damage, such as Hurricane Mitch in 1998, Hurricane Keith in 2000 and Hurricane Iris in 2001.

A preliminary trip to Belize was conducted in March 2000 in order to select a suitable study area. Three regions were visited: Bacalar Chico off the northern coast, the Turneffe Islands off the mid-point of the coastline and Punta Gorda on the southern coast (Figure 1.5).

The town of Punta Gorda in the Toledo District is the administrative centre for Port Honduras, which has recently been granted marine reserve status. Toledo District currently has an Integrated Conservation and Development Project, funded by USAID and The Nature Conservancy, and co-ordinated by a local Non Government Organisation, the Toledo Institute for Development and Environment (TIDE). The project covers the Gulf of Honduras basin, an area of approximately 10,000 square kilometres. Fieldwork would have been conducted in association with TIDE, which has extensive laboratory facilities. Although well suited logistically, Punta Gorda was unsuitable in physical terms, having high rainfall and turbidity relative to the remaining two areas. As fieldwork would have to be undertaken during the period of the year with the highest rainfall, an area with low rainfall would have been preferable.

Bacalar Chico became a Marine and Wildlife Reserve in 1996 when it achieved status as a World Heritage Site. Covering a total area of approximately 100 square kilometres, there are extensive tracts of easily accessed mangroves throughout the reserve, which is well protected by the barrier reef. Accommodation is available at the ranger's station at San Juan on the western side of Bacalar Chico. With a low rainfall, the area was well suited physically. However, it was less suitable for the present study in terms of logistics, as there are no laboratory facilities and fieldwork would have to be co-ordinated with the daily duties of the rangers.

The Turneffe Islands atoll is located 51 km off the Belize coast and east of the Belize Barrier Reef. Approximately 60 km long by 16 km wide, it consists of over 200 low-lying mangrove cays and sand banks within its own reef, which is surrounded in turn by deep water. Most of the atoll is not protected by legislation, and it is a well-known fishing and scuba-diving site. The University of Belize (UB) has an Institute of Marine Studies (IMS) at Calabash Cay, with good laboratory facilities.

As the institute functions purely as a research station, good logistical support is available to researchers. Rainfall and turbidity are relatively low compared to the Belize mainland.

Of the three areas visited, Calabash Cay in the Turneffe Islands (Figure 2.1), was found to be the most suitable when considering both physical and logistical aspects, and was selected as the specific study area.

Turneffe is separated from the barrier reef by a 10-16 km wide channel averaging 250 m in depth. Unlike Glovers and Lighthouse Reefs, which are open to the ocean and have normal marine circulation, the lagoons of Turneffe have a restricted circulation and few patch reefs. Extreme fluctuations in water temperature and salinity have been observed, with maximum values of 31 °C and 70 ‰ respectively in the southern lagoon (Gischler & Hudson, 1998). Southward currents flow between the atoll, and the barrier reef and Lighthouse Reef (Purdy *et al.*, 1975). In the interior lagoons of the atoll, which are up to 8 m in depth, water currents flow west, creating a westward drift. The lagoon floors are almost entirely covered by seagrass beds, dominated by the broad-leaved turtle grass *Thalassia testudinum*. The finer manatee grass *Syringodium filiforme*, and algae of the *Halimeda* genus are also widely distributed in the atoll lagoons. The land of the southern half of the atoll consists mainly of the mangrove *Rhizophora mangle* L., known commonly as red mangrove.

There is a well-defined narrow reef on the windward, eastern side. The reef crest is narrow and fringes the outer edge of a reef-flat less than 400 m wide. The reef is highly segmented, with about 23 gaps, or channels, most of which are less than 50 m wide and 6 m deep. Small sandy cays are located between the channels on the inner edge of the eastern side of the reef flat; one of these is Calabash Cay. The windward side of the cays close to the reef crest are flushed by large

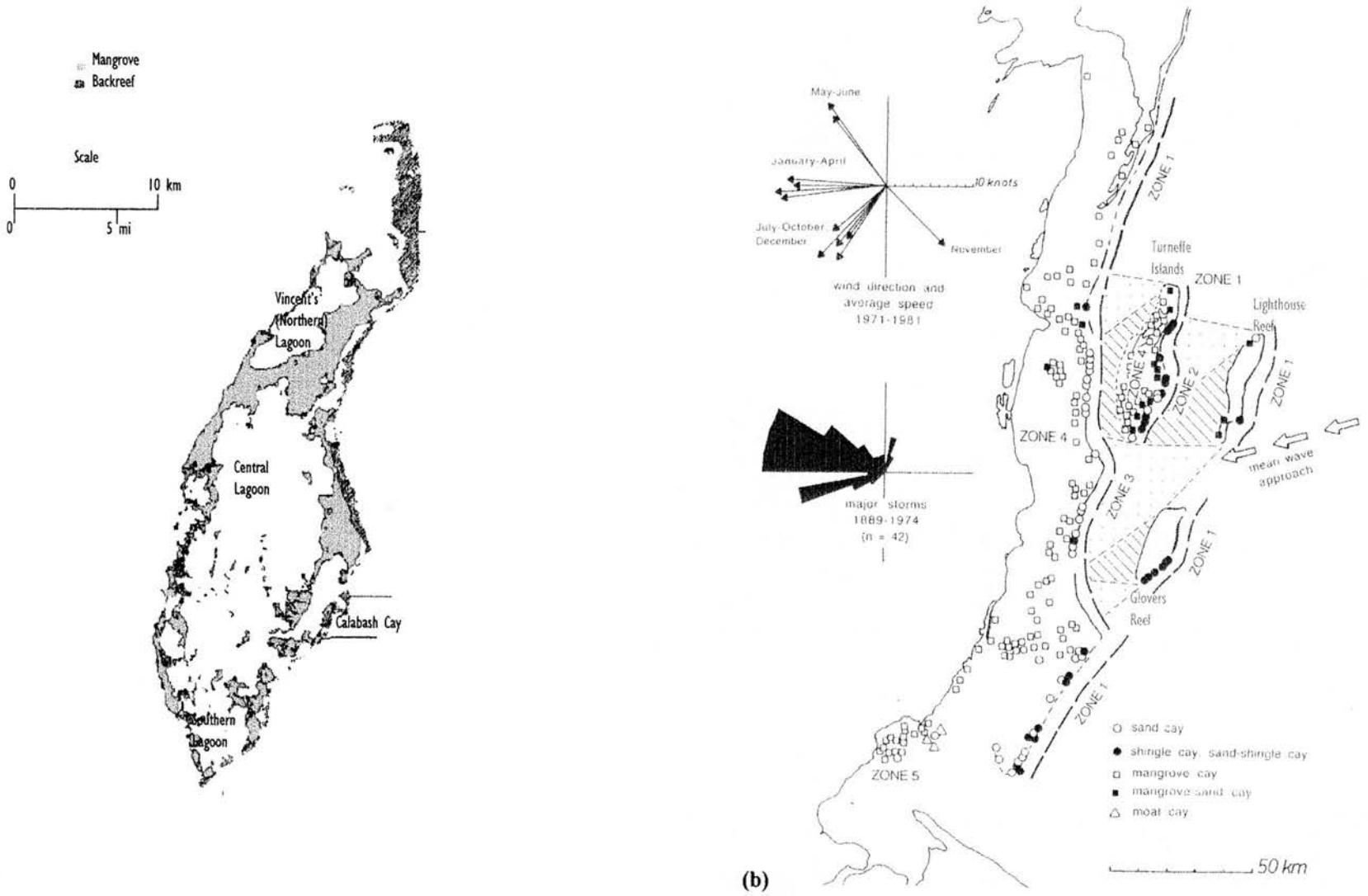


Figure 2.1. (a) Location of Calabash Cay on Turneffe Islands atoll, with mangrove and backreef. (b) Wave sheltered positions of Turneffe Islands due to Lighthouse Reef (from Gischler & Lomando, 2000). Stippled areas: modified wave force; hatched areas: maximum impedance of wave force. Wave energy: Zone 1, maximum and submaximum; Zone 2, high; Zone 3, medium; Zone 4, low; Zone 5, moderate.

amounts of seawater, while the northern part of the atoll is open to the Caribbean Sea and consequently receives the maximum wave force (Gischler & Lomando, 1997). The mean wave approach is from ENE , with current velocities ranging from 1.8 to 3.6 kmh^{-1} (Burke, 1982). The major part of Turneffe Islands is protected from the open Caribbean Sea by Lighthouse Reef to the east, and is only exposed to reduced wave forces.

The northern lagoons have a good circulation, sparse mangrove cover and abundant patch reefs. Vincent's Lagoon is a designated marine reserve and the only area of the atoll that is currently protected by legislation. Three small-scale exclusive resorts are situated on the eastern and southern sides of the atoll: Turneffe Flats Lodge, Blackbird Cay Resort and Turneffe Island Lodge. A fourth is under construction on Calabash Cay (Figure 2.2). The remainder of the atoll's inhabitants are fishermen and their families, living in both permanent and temporary camps throughout the cays.

Figure 2.2. An aerial view of Calabash Cay. IMS = the Institute for Marine Studies, run by the University of Belize.

The aerial view of Calabash Cay in Figure 2.2 shows its dense vegetation cover, which consists predominantly of the mangrove *Rhizophora mangle* L.. The sheltered nature of the inner waters of the lagoons and the extensive network of canals through the mangroves make it ideal for observational work. The atoll also has the physical

advantages that it is unaffected by terrestrial processes from the mainland and therefore the hydrology is likely to be less complicated with fewer terrestrially derived inputs. The average precipitation of Belize's atolls amounts to 500 mm/year, in comparison to the range of 1240 mm/year in the north of mainland Belize to 3800 mm/year in the south of the country (Stoddart, 1962; Purdy *et al.*, 1972). The tidal range is 0.5 m with water temperatures ranging between 29°C in summer and 26°C in winter.

2.2. *Survey methods*

Calabash Cay was arbitrarily divided into three regions to accommodate a nested sampling design, based on natural separations between continuous stands of mangroves (Figure 2.3).

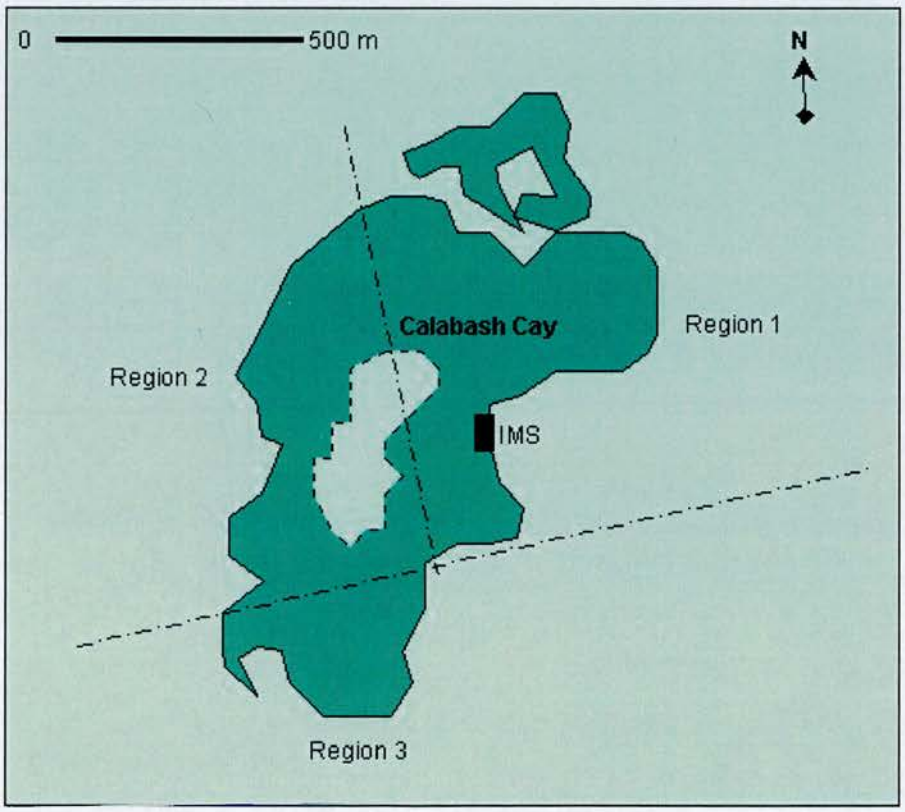


Figure 2.3. The division of Calabash Cay into three sampling areas, referred to as Regions 1, 2 & 3. IMS = Institute for Marine Studies.

The main aim of the research project was to examine the spatial and temporal distribution of the different life stages of fish populations within the mangroves and adjacent habitats of Calabash Cay. Three

main survey methods were used within the nested sampling design to cover differing spatial scales, and over a period of several months to cover a wide temporal scale. To sample the larval stages of fish present in the mangroves and adjacent habitats, both a passive and an active method of collection were used. These were light traps and plankton nets respectively. A non-invasive visual census survey method was used to sample juvenile and adult populations.

2.2.1. Plankton nets

During the first field season samples were collected by plankton net during daylight on four separate dates to cover a whole tidal cycle: the 3rd, 12th and 21st August and 2nd September 2000. On each date, two plankton nets were used in tandem, one with 250 um mesh, the other with 118 um mesh (Figure 2.4).

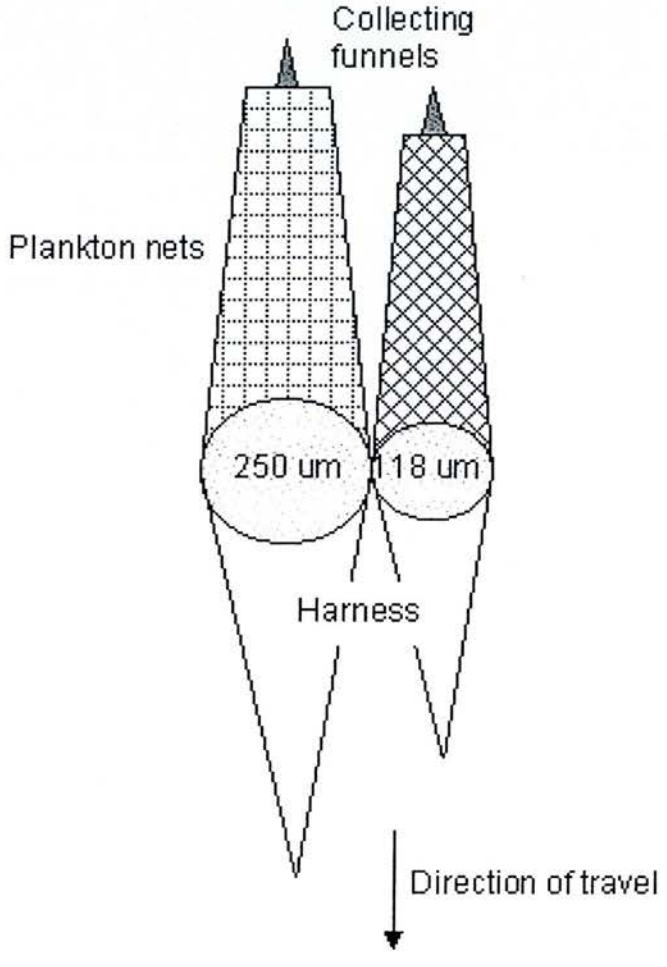


Figure 2.4. Plankton nets with mesh size 250 um and 118 um respectively were pulled in tandem parallel to the boat/sampler by the harness.

Each plankton net trawl was for a period of up to 5 minutes. Samples were collected from the nets by removing the codpiece on the end of each net, and washing the contents into a sorting tray using 500 ml of filtered seawater per sample. Each sample was then placed in a labelled plastic bag, and kept in a cool dark area of the boat until taken to the IMS. At the IMS all samples were processed as described in Section 2.2.3.

A flow meter was held at the mouth of the plankton nets during tows, and the count for each tow recorded. The time of each tow to the nearest second was also recorded. From these two figures, the flow rate (v, in centimetres per second) of water through the plankton nets was calculated using the equation:

$$v = (0.144 \times C) + 5 \qquad \text{- Equation 2.1}$$

where C = flow meter count/60 seconds

Subsequently the volume (V, in cubic centimetres) of water passing through each net during each tow was calculated using the equation:

$$V = v \times T \qquad \text{- Equation 2.2}$$

where v = flow speed in cm/s

T = duration of tow in seconds

A nested sampling design was used, with three Regions approximately 1 km apart each containing three Stations approximately 100 m apart (Figure 2.5). At each station, three plankton net tows were conducted in the mangroves, and three parallel to the mangroves approximately 100 m offshore.

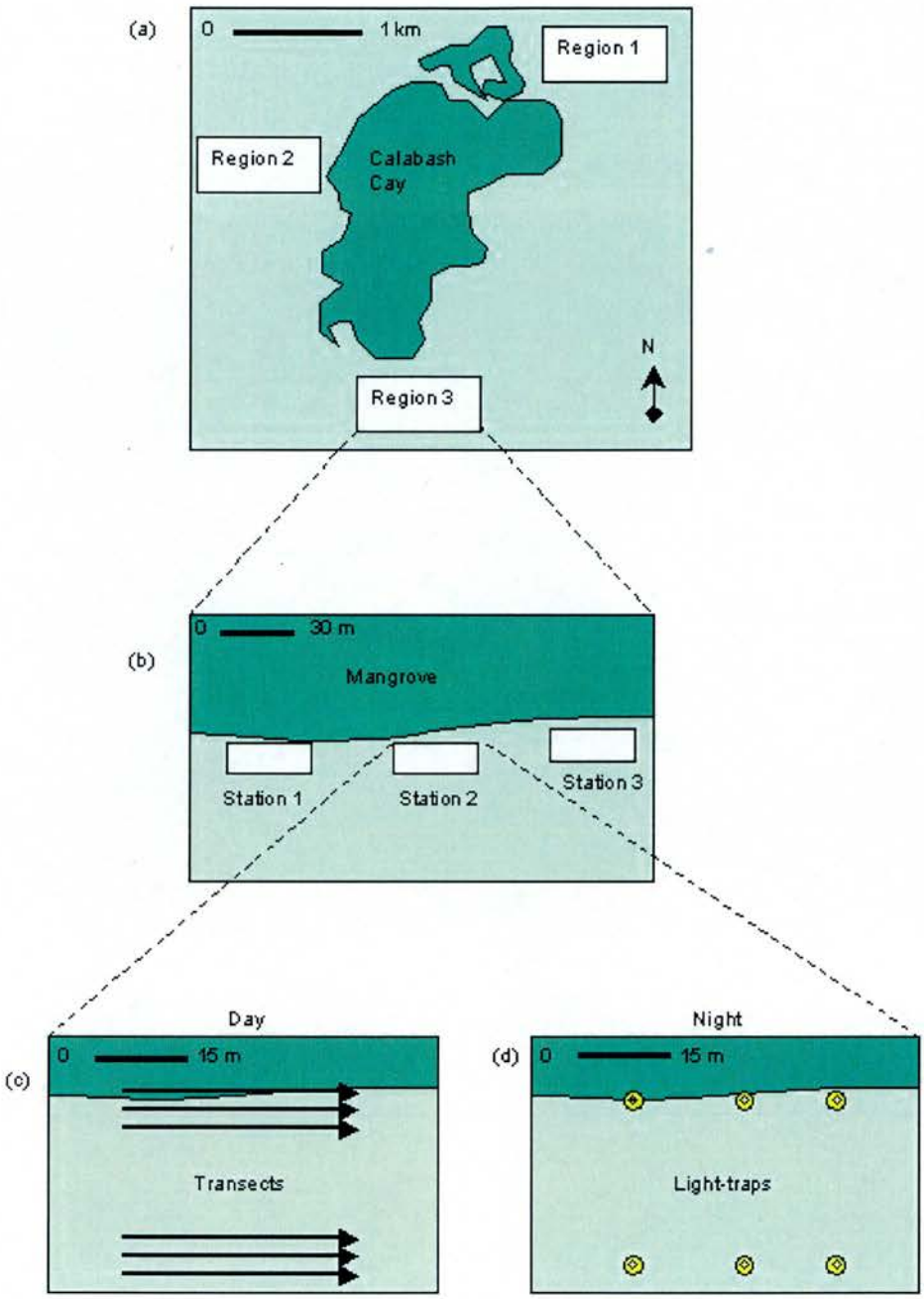


Figure 2.5. The nested sampling design used at Calabash Cay. The three Regions as shown in (a) represent the survey areas. Within each Region there are three stations as shown in (b), approximately 100 m apart. At each station, 3 plankton net tows are conducted in the mangroves, and 3 parallel to the mangroves approximately 100m offshore as in (c). At night, 3 light-traps are set along each transect line, as shown in (d).

Within each region, a total of 9 samples was taken in the mangroves at each station, and 9 samples 100 m offshore in the adjacent seagrass habitat, with a 250 um mesh plankton net. A 118 um mesh plankton net was used in tandem with the 250 um mesh net at each station to collect a further 9 samples in the mangroves, and 9 samples 100 m

offshore in the neighbouring seagrass habitat. On a single date this gave 36 samples from each Region, and a total of 108 samples from the whole of Calabash Cay.

Initial analysis of results from the first field season indicated that the plankton net tows were not collecting plankton efficiently, as the numbers observed in samples were very low. The most probable causes of this were surmised to be the speed of the tows or the length of time spent towing. Accordingly a trial was run using both longer tows and differing the speed of tows. It was found that longer tows gave better results in the form of higher numbers of organisms per sample, and the speed of towing as used previously was optimal.

In order to accommodate longer tows into a single sampling period of one day, a level of replication as shown in Figure 2.5 was removed. Instead of having 3 sets of 3 x 100 m long replicate tows in each habitat at each station (Figures 2.5c, 2.5d), it was decided to do 1 set of 3 replicate tows across all three stations. In the second field season running from June 2001 to November 2001, a third net was added and the three nets were placed in a frame (Figure 2.6).

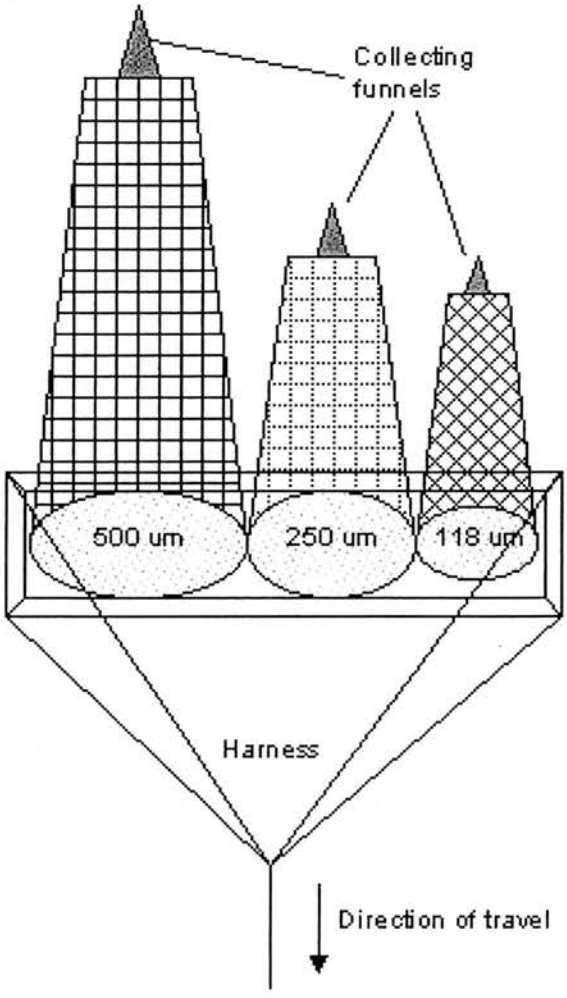
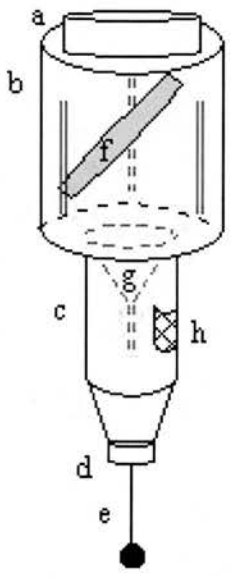


Figure 2.6. Plankton nets with mesh size 500 um, 250 um and 118 um respectively were held in a frame and pulled in tandem parallel to the boat by a harness.

2.2.2. Light traps

To collect samples during the night, light-traps based on designs developed by ICLARM (Watson *et al.*, 2002) were used. Each trap consists of a main body (b) of 2-litre volume, with a screw lid (a) through which the light source (f) can be inserted and removed. The light source consists of a 15-watt output fluorescent bulb powered by 4 AA batteries, with a total running time of 4 hours. The light source is kept waterproof by a double layer of ziplock bags, the seals of which are coated in vaseline.



a - Screw lid
b - Main body with 3 vertical 10 cm long slots each 0.5 cm wide. Volume 2 l
c - Collecting bottle. Volume 1 l
d - Screw lid
e - Weighted line
f - 15 watt output fluorescent light in double ziplock bags
g - Funnel connects main body to collecting bottle
h - Draining window with 118 um mesh netting

Figure 2.7. Plan diagram of light-trap.

Zooplankton attracted by the light source enter the main body through one of the 3 vertical slits, which are 0.5 cm wide and 10 cm long. On reaching the light, organisms stop actively swimming and float downwards, descending through the funnel (g) into the collecting bottle (c). Each light trap is set for 2 hours, kept in position by a weighted line (e) and marked by an attached float. The natural buoyancy of the trap, which is constructed from plastic, keeps the structure more or less vertical. On removal, water drains down through the funnel and out of the draining window (h), pulling any zooplankton in the main body with it. All organisms larger than 118 um are then retained in 500 ml of seawater remaining in the collecting bottle. The collected sample is then emptied with ease into a labelled plastic bag by removal of the screw lid (d). Each trap has a light radius of approximately 5 m. The back of each lighting unit is opaque, with the result that light shone in an arc to one side of the lighting unit.

At night, three light-traps were set along each transect line (Figure 2.5d). Thus at each of the stations (Figure 2.5b) there were three light-traps within the mangroves, approximately 30 m apart, and three light-traps 100 m offshore from the mangroves, opposite the first three. A total of 18 light-traps were set in this manner per Region. It was not

logistically possible to have 18 traps set in each region simultaneously, as only one boat was available and the boat could only carry 18 traps. Due to this, the 18 light-traps were set in a single Region for 2 hours, then retrieved, emptied and re-set in another Region for 2 hours, then retrieved, emptied and re-set in the final Region for 2 hours. Approximately 30 minutes were required to set out all 18 traps in one region, and up to one hour was required for their retrieval.

In between setting and retrieving the light-traps, collected samples were taken back to the Research Station to be processed. The first traps were set at 19:00, shortly after sunset, and the third set of traps were retrieved around 03:00, approximately an hour before sunrise. At the time of setting the traps, cloud cover and state of the moon were recorded. The GPS reading and water depth were recorded at each light-trap. The order in which Regions 1, 2 and 3 were sampled was decided through the use of random number tables.

2.2.3. Sample processing

The processing of the samples was based on standard techniques, such as those described by Smith and Richardson (1977), and consisted of three main stages: preservation, sorting and identification.

Preservation commenced with the addition of a few crystals of chloral hydrate to each sample as soon as possible after collection, to narcotise the organisms. Once the chloral hydrate had taken effect, usually a period of 10-15 minutes, each was then fixed with 5% formaldehyde solution and left for 24 hours. Additional buffer was not added to the formaldehyde, as the seawater acted as a natural buffer. If a lot of detritus was present in samples taken by plankton net, a few drops of Biebrich's scarlet were also added to enable easier detection of organisms.

Following fixation in formaldehyde for 24 hours, each sample was filtered out of solution using a 118 um mesh filter, and soaked in deionised water for 10 minutes. It was then rinsed twice with deionised water, and finally placed in 70% isopropan-2-ol in 10 ml plastic containers. The samples could then be stored indefinitely, although occasional changes of the storage solution would be required to prevent the samples becoming too acidified.

The samples were 'sorted' into separate categories of fish larvae and invertebrate larvae as soon as possible after preservation, usually within a month after collection. Samples were examined under a dissection grade microscope, and all fish larvae removed and placed in separate containers in fresh 70% isopropan-2-ol. The remaining larvae were sub-sampled if more than 10 ml of organisms were present, in order that up to 10 ml of invertebrate larvae were retained for future examination.

Following separation from the remainder of the sample, fish larvae were identified as far as possible using general references such as Leis & Carson-Ewart (1999) and more specific references such as Richards *et al.* (1974), and a reference collection composed with the help of Dr. William Richards of the Miami Fisheries Department, Miami, Fl., using some of the actual samples collected. Dr. Richards, Dr. David Smith at the Smithsonian Institution, and Kerryn Parkinson at the Australian Museum confirmed final identification.

2.2.4. Visual fish census

Juvenile and adult fish assemblages were characterized and quantified using a modification of the visual belt-transect census method of Rooker & Dennis (1991). A visual census was carried out in each station of each region either a day before or a day after the daytime and nighttime collections. A single individual conducted each census, thereby ensuring uniformity through lack of observer bias. Each

census consisted of three consecutive 10 minute snorkel surveys parallel to the shore along each set of transect lines (Figure 2.5c). Each snorkel survey was slow but conducted at a steady pace, and covered a distance of approximately 30 m. The belt transect width was 1 m, making the area surveyed per transect 30 m^2. The identity, number and size-structure of fishes was observed and recorded.

Juvenile fish are defined as individuals that have not yet reached sexual maturity. As no evidence exists to date for the size at which fish species in Belize reach maturity, means were taken from Austin & Austin (1971), Humann (1999), García-Cagide *et al.* (2001) and Serafy *et al.* (in press).

2.2.5. Habitat surveys

Habitat surveys were conducted along each of the transect lines used for the plankton net and light trap surveys. Slightly differing survey methods were required in the seagrass beds and mangrove stands, based on techniques described by English *et al.* (1997) and Nagelkerken *et al.* (2000b) respectively. In both habitats each single transect of approximately 100 m was surveyed using 5 quadrats spaced at regular intervals of 20 m.

In the seagrass beds a 50 cm square quadrat was placed across the transect line at each survey point and water depth at the centre of the quadrat recorded. Within the quadrat the observer recorded the area occupied by cover material (i.e. not bare substrate) as a percentage. The total percentage was then divided into its individual components, of which all plants were identified to species level where possible, to give the percentage of the quadrat area covered by each individual species of plant. For each species of seagrass the total number of leaves and their mean height were recorded.

In the mangrove stands a 1 m square quadrat was placed across the transect line at its starting point and water depth at the middle of the quadrat recorded. Within the quadrat the length and diameter of each root was measured. Where the roots of the stand were accessible to a width of more than 1 metre, successive quadrats were laid into the mangroves from the first quadrat, perpendicular to the transect line. The water depth, length and diameter of each root were recorded as in the first quadrat.

2.2.6. Physical parameters

In situ physical measurements were taken immediately after each plankton net tow. A water sample was taken 50 cm below the water surface using a plastic bottle, and it's temperature measured using a mercury thermometer. Light intensity was measured at the surface of the water and 50 cm below, with a hand-held light meter, and used to calculate the extinction coefficient (***E***):

$$E = 2.30 \log (I_0/I_d)/d \qquad \text{- Equation 2.3}$$

where d is the depth at which the measurement is taken

I_d is the light intensity at that depth

I_0 is the light intensity at zero depth or just below the surface

Water depth was measured at the either end of the transects using a 2 lb scuba diving weight attached to the end of a tape measure. Wind speed and direction were measured using a hand-held anemometer.

Water samples of 500 ml were taken with each plankton net tow and retained in plastic bottles. At the IMS the pH of each water sample was measured using a pH meter. Salinity was measured using a hand-held salinometer. A portable palintester was used to calculate sulphate, sulphite, nitrate and nitrite ion concentrations, and the turbidity of each sample.

2.3. *Experimental testing of light-trap sampling duration*

Previous research has generally assumed that the sampling duration and the time of night at which sampling is undertaken makes no significant difference to the abundance of larvae in a light trap sample (Watson *et al.*, 2002; Choat *et al.*, 1993; Brogan, 1994). To test these assumptions, a hierarchical study was conducted over 3 weeks in August 2001, at Calabash Cay.

Two light-traps of similar design were set out approximately 15 m apart over seagrass beds 20 m offshore, in water depth of 1.5 - 2 m. Both traps were set for 3 consecutive 2-hour periods in a single night, with the first period commencing at approximately 19:00. Each trap was removed from the water for 10 minutes between successive sampling periods to retrieve the samples and allow re-dispersal of organisms in the water column. Sample collection was repeated for 3 consecutive nights in each of the three weeks. The samples were processed and identified as described in *2.2.3 Sample processing*.

2.4. *Statistical analysis*

2.4.1. Relative abundance

The counts of fish larvae collected by plankton-net tows during the day were converted to a density figure of larvae per 100 cubic metres of water for analysis, while those collected at night were analysed as number of larvae per trap. Juvenile and adult fish abundances recorded using visual surveys were analysed as number of fish per 30 square metres.

Spatial and temporal comparisons of larval, juvenile and adult fish counts were conducted using parametric and non-parametric statistical tests, in the computer software package MINITAB™. Null hypotheses were rejected when the level of the probability value, p, associated with

the test statistic was 0.05 (5 %) or less. Prior to testing, abundances were examined for equal variance and normal distribution (Zar, 1984). Where equal variance and normal distribution were not achieved, counts were $\log_{10}$ transformed. If normality and equal variance were achieved, parametric analysis was used to compare mean counts. For comparison of two samples, a T-test was employed to give the statistic T and associated probability value, p. For comparison of more than two samples, analysis of variance (ANOVA) was used to give the statistic F and associated p-value. Where a significant p-value (≤ 0.05) was achieved, a Tukey's pairwise comparison was conducted. Where normality was not achieved, non-parametric analysis was used to compare median counts. If variances were equal, a Kruskal-Wallis test was employed to give the test statistic H and associated p-value. If variances were not equal, a Mood's median test was used to give the test statistic χ^2 and associated p-value.

To test the degree to which counts varied, correlation analysis was used. This produced the Pearson correlation coefficient, r, which ranged from –1.0, indicating a perfect negative correlation, to + 1.0, indicating a perfect positive correlation. Correlation was deemed significant at an associated p-value of ≤ 0.05.

2.4.2. Assemblage composition

Analysis of spatial and temporal variation in the taxonomic composition of the larval, juvenile and adult fish assemblages was conducted using parametric and non-parametric statistical tests in the computer software package PRIMER v5 (Plymouth Routines in Multivariate Ecological Research). Univariate methods were used to calculate diversity index values for samples. These, the Shannon diversity index, H', and Margalef's index of species richness, d, were used for further analysis by ANOVA.

The multivariate methods used by the PRIMER package are founded on similarity coefficients calculated between each pair of samples. Therefore the comparison of samples is based on the extent to which the samples share species, at comparable levels of abundance. Similarity coefficients then enable the clustering of samples into similar groups, or ordination plots, in which samples are mapped in two or three dimensions in such a way that the distances between pairs of samples reflect their relative dissimilarity of taxonomic composition (Clarke & Warwick, 1994). In the present study, hierarchical agglomerative clustering (CLUSTER) was used, in which samples are successively fused into larger groups as the criterion for the similarity level defining group membership is relaxed, and two ordination techniques: principal components analysis (PCA) and non-metric multi-dimensional scaling (MDS). CLUSTER and MDS start from a triangular matrix of similarity coefficients computed between every pair of samples. The Bray-Curtis coefficient, also referred to as the Czenowski coefficient, is used by PRIMER (Clarke & Gorley, 2001). A level of 100 % represents total similarity and 0 % complete dissimilarity. To remove the emphasis of rare species on the patterns of CLUSTER and MDS, data was fourth root transformed prior to analysis.

For the clustering technique, communities for each sample are represented in a dendrogram. Taking the similarity matrix as the starting point, samples are fused into hierarchical groups and the groups into larger clusters, starting with the highest mutual similarities then gradually lowering the similarity level at which groups are formed. The process ends with a single cluster containing all samples. One axis of the resulting dendrogram represents the full set of samples, the other defines a similarity level at which two samples or groups have fused. Links between the groups may be single (also called nearest neighbour), complete (furthest neighbour) or group-averaged. Single linkage is simply the minimum distance apart of any two samples in

two groups, complete linkage is the maximum distance apart, and group-average is the average distance apart of the two groups. Group-averaging was favoured here, as it strikes a balance in which a moderate number of medium-sized clusters are produced, and only grouped together at a later stage.

While cluster analysis attempts to group samples into discrete clusters, ordination displays their inter-relationship on a continuous scale. The method of non-metric MDS constructs a configuration or map of the samples, usually in two dimensions, in such a way that the rank order of the distances between samples on the map exactly agrees with the rank order of the matching (dis)similarities, taken from the triangular similarity matrix. For example, if sample 1 has a higher similarity to sample 2 than it does to sample 3, then sample 1 will be placed closer on the map to sample 2 than it is to sample 3. The use of rank order information about sample similarity means that direction in the MDS plot cannot be interpreted as the absolute distance apart of two samples, rather should be interpreted as relative values. Success is measured by a stress coefficient, which reflects the extent to which the two sets of ranks do not agree. For 2-dimensional ordinations, stress values of $\leq$ 0.2 correspond to good ordinations with a low prospect of a misleading interpretation (Clarke & Warwick, 1994). If successful, the ordination gives a simple visual representation of closeness of the species composition of any two samples.

The PCA technique uses the original data matrix rather than a derived similarity matrix. However, it also results in an ordination plot, usually in two or three dimensions, which approximates the continuum of relationships between samples. The definition limits of PCA are relatively inflexible, making it more useful for multivariate analysis of environmental data rather than species abundances (Clarke & Warwick, 1994).

Multi-species abundance data typically does not satisfy the assumptions required (i.e. normality) for conventional ANOVA or analogous multivariate analysis of variance (MANOVA). Instead, a valid test built on a simple non-parametric permutation procedure and applied to the (rank) similarity matrix underlying the ordination or classification of samples is used, and termed an ANOSIM test (analysis of similarities) by analogy with the acronym ANOVA. The PRIMER program ANOSIM tests replicates from 1-way and 2-way (nested or crossed) layouts.

Further information on sample similarities is gained from highlighting the species principally responsible for determining the groupings in the cluster or ordination analyses. One way of achieving this is to calculate the Bray-Curtis dissimilarity between all pairs of inter-group samples (i.e. every sample in group 1 paired with every sample in group 2), compute the average dissimilarity and break it down into the separate contributions from each species (Clarke & Warwick, 1994). This is implemented by the PRIMER program SIMPER (similarity percentages), both in respect of contributions to average similarity within a group and average dissimilarity between groups.

2.4.3. Linking assemblage composition to environmental variables

For analysis of environmental variables, Euclidean distance is an appropriate measure of dissimilarity and PCA is an effective ordination technique. As the samples are replicates from different groups defined *a priori*, any differences between sites or times can be established with ANOSIM tests, using Euclidean distances for the appropriate (rank) dissimilarity matrix. Community structure is then related to multivariate descriptions of the abiotic variables using non-parametric similarity-based methods.

If a suite of environmental variables responsible for structuring the community is known, then samples having similar values for these variables would be expected to have similar species composition, and an ordination based on the abiotic data would group sites in the same way as for the biotic plot. If key environmental variables are omitted, the match between the plots will deteriorate, and by the same rationale the match will worsen if abiotic data irrelevant to the community structure are included. To quantify the match of biotic to environmental patterns, the ranks of the similarity matrices underlying the biotic and abiotic ordinations (Bray-Curtis and Euclidean distance respectively) are compared through a rank correlation coefficient. The PRIMER program BIOENV gives a standard Spearman rank correlation coefficient, ρ, and indicates which environmental variables maximise the matching coefficient, to pinpoint any potential causal relationships.

2.4.4. Linking suites of assemblage composition data

As for the analysis of the links between environmental variables and assemblage composition, a rank correlation concept is used to compare two similarity matrices of biotic data for a matching set of times, or sites, to establish which assemblages show a similar pattern of variation. If the among-sample relationships are the same, the rank correlation $\rho = 1$, indicating a perfect match. Such calculations are performed using the PRIMER program RELATE, which applies a significance test to the matching coefficient ρ. The same routine is used to assess the extent to which samples follow a simple trend or seriation, such as a linear sequence in time or space. In such a case, adjacent samples are closest in species composition, samples two steps apart the next closest, etc., with the first and last samples being the most distant in assemblage composition.

3.0 The relative abundance of the larval, juvenile and adult life history stages of Caribbean reef fish taxa from a mangrove island

3.1 *Introduction*

Many species of fish are known to spend their different life stages in different habitats and different geographical areas, perhaps migrating for 100s or 1000s of miles. Adult fish in particular will migrate to spawning grounds far away from their home ground, with the result that the larval and juvenile populations do not always reflect the local adult population. While spawning grounds are often well known, in particular by fishermen, the dispersion of fish larvae and eggs, and the subsequent recruitment of juveniles, remains an area of ongoing research.

Mangroves and seagrass beds have been shown to contain a high diversity and abundance of fish in the Caribbean (Austin, 1971; Thayer *et al.*, 1987; Baelde, 1990; Sedberry & Carter, 1993). However, many studies focus on a single methodology and as a result a single life stage, for example by not distinguishing between adult and juvenile fishes. There is little quantitative or qualitative data of larval, juvenile and adult fish for the mangrove and seagrass habitats of the Caribbean (Dennis, 1992; Nagelkerken, 2000), and for Belize in particular (Sedberry & Carter, 1993).

As a result, the extent to which young and adult stages of marine organisms depend on these habitats is not clearly understood. This is especially so in the case of oceanic islands, where the shallow water habitats generally have a lower turbidity and greater circulation than mainland coasts (Dennis, 1992). Few fish species have been identified as obligate users of mangroves and most are assumed to have a facultative mangrove dependency. The full relationship of fish with

the mangrove habitat can only be accurately assessed through analysis of all three life stages in the same geographical area. When considered with the habitat structure, the most probable selective pressures, i.e. availability of food or shelter, or level of predation, and so the level of dependency of individual species on their habitat, may be better understood. The first step is to establish the taxonomic composition of the larval, juvenile and adult stages of fishes present in the shallow water habitats.

3.2 *Results*

3.2.1 Taxonomic composition of each life-stage assemblage

A distinct difference is apparent between the larval, juvenile and adult life stages, based on presence/absence of taxa in the assemblages of the three stages, and between the night and day collections of larvae (Figure 3.1). The species composition of the assemblages does not vary significantly, however (ANOSIM: R = 0.694, p = 0.067).

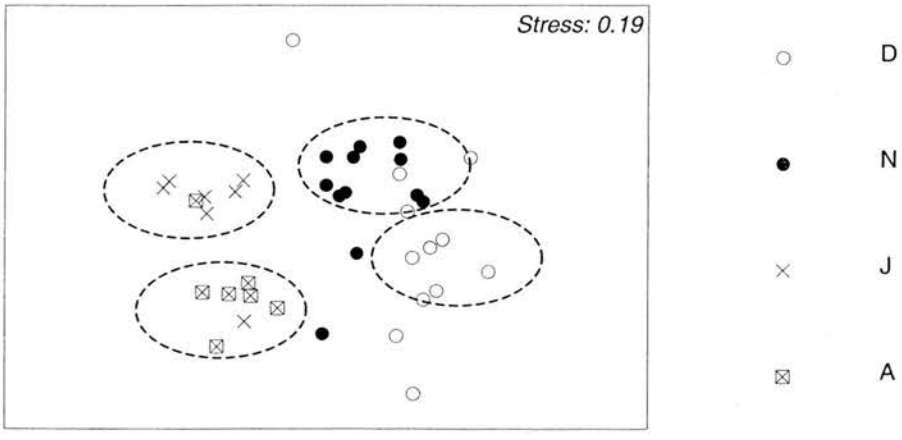


Figure 3.1. A non-metric MDS ordination plot of the day (D) and night (N) larval assemblages, and the juvenile (J) and adult (A) fish assemblages, based on Bray-Curtis similarity indices of presence/absence of family. Individual points represent assemblage composition on each sampling date for both seagrass and mangrove habitats of Calabash Cay. Strong grouping of each assemblage type is evident along the horizontal and vertical axes, and is supported by CLUSTER analysis, as shown by the dashed lines representing 50 % similarity grouping.

A total of 159 species or types of fish from 50 families were recorded from the mangrove and adjoining seagrass habitats of Calabash Cay (Appendix 3.1, 3.2). The larval stages of 120 species or types in 44 families were identified from collections made during the day by plankton net and at night by light trap. The larval assemblage in the seagrass habitat, representative of the supply of larvae to the mangroves, is relatively similar to the larval population of the mangrove habitat in terms of the total number of species (Figure 3.2).

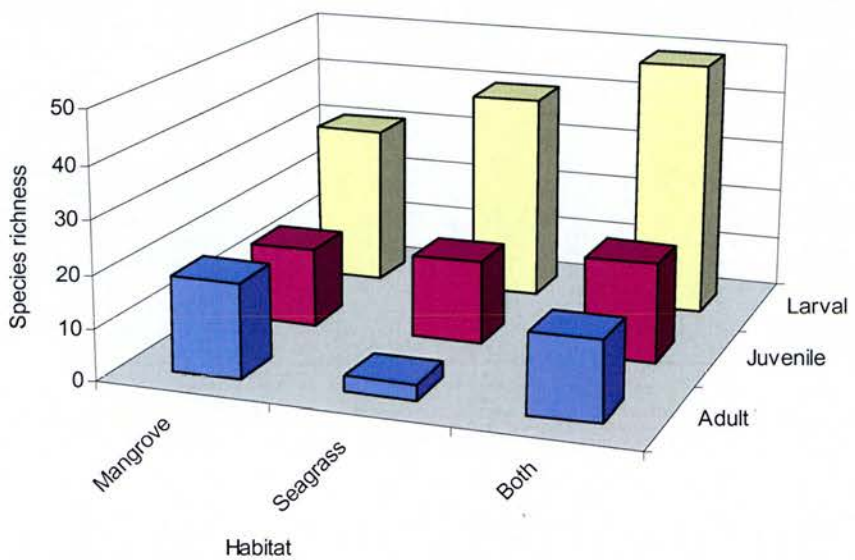


Figure 3.2. Species richness of larval, juvenile and adult assemblages in the mangrove and seagrass habitats of Calabash Cay. The greater species richness of larvae in the seagrass than mangrove shows the larval supply to the mangroves exceeds the resident larval population. In the seagrass a decrease in number of species from the larval to juvenile to adult stages indicates loss of larvae and juveniles through emigration or death. In the mangroves a decrease is also evident between the larval and juvenile stages, but not between the juveniles and adults.

Larval species richness is qualitatively greater in the seagrass assemblage than that of the mangroves (Table 3.1). The predominant species are *Atherinomorus stipes*, Blennioidei Types C, D and E, and *Hypoplectrus* sp. (Appendix 3.1). In the mangroves *A.stipes*, Blennioidei Type D, *Jenkinsia parvula*, Clupeidae Type A, *Gobiesox punctulatus*, *Bathygobius soporator*, *Gobiosoma* sp. and *Hypoplectrus* sp. dominate. As the adults of *A.stipes*, *J.parvula* and clupeids all

occur in large shoals, high numbers of the larval and juvenile stages are also expected.

A similar pattern of species richness is evident for the juvenile assemblage, in which a total of 50 species or types in 20 families were identified during the visual census surveys (Figure 3.2). However, the species richness in the seagrass habitat only exceeds that of the mangroves by a single species (Table 3.1). Both the larval and juvenile stages appear to have a similar distribution of species, with approximately a third of species present in the mangroves, a third in the seagrass and a third across both habitats.

Table 3.1. Species richness of larval, juvenile and adult assemblages in the mangrove and seagrass habitats of Calabash Cay. Number of species is followed by number of families in parentheses. The marked decrease in the number of species from the larval to the juvenile and adult stages suggests an initial high influx of larvae is followed by loss through emigration of older stages or death. The relatively low number of adult species recorded solely in the seagrass suggests few if any adults have an obligate dependency on that habitat.

	Habitat		
	Mangrove	Seagrass	Both Mangrove & Seagrass
Species richness:			
Larval	31 (8)	40 (11)	49 (25)
Juvenile	15 (5)	16 (5)	19 (10)
Adult	18 (7)	3 (3)	15 (9)

The juvenile assemblage of the mangrove habitat is dominated by *Haemulon flavolineatum*, *Atherinomorus stipes*, *Strongylura notata*, *Lutjanus apodus*, *Lutjanus griseus* and *Scarus* sp. (Appendix 3.1). In the seagrass beds *H.flavolineatum* is also relatively abundant, along with *Haemulon sciurus, Acanthurus* sp., *Eucinostomus argenteus*, *Halichoeres* sp. and *Scarus* sp., the last of which constitutes over a third of the juvenile seagrass assemblage.

There is a noticeable change in the number of species between the larval and juvenile stages, with the species richness dropping by 50 %

or more. This suggests that larvae are either emigrating from the mangrove and seagrass habitats, or being removed through predation, starvation or disease. A major proportion of the larvae, approximately 50 and 60 % in the mangrove and seagrass respectively, are ≤ 0.5 cm in length and therefore only a few days old. As the larval stages of tropical fishes generally have a short duration of a few weeks, the extensive temporal scale on which the present study was conducted would be expected to detect the successive early life stages of many fish species, where present.

The overall species richness drops again for the adult fish assemblage (Figure 3.2), with a total of 36 adult species or types in 19 families recorded. In a marked difference to both the larval and juvenile stages, the number of species or types in the mangroves exceeds that of the seagrass by six times (Table 3.1). In addition, the species richness of the adults' mangrove assemblage is greater than that of the juveniles, a departure from the general pattern. The mangrove habitat may be more suitable to a wider range of adult species than the seagrass beds in terms of the amount of available shelter, which is generally greater in the former.

Approximately a quarter of the adult assemblage in the mangrove habitat is accounted for by *Atherinomorus stipes*, a schooling species. However, all shoals of over 150 individuals have been excluded from the analysis to prevent severe skewing of the data. *Lutjanus apodus*, *Lutjanus griseus*, *Haemulon flavolineatum*, *Haemulon sciurus* and *Scarus* sp. are also predominant. In the seagrass habitat *Scarus* sp. account for almost a third of the adults, with *Halichoeres* sp., *Sparisoma* sp., Gobiidae Type A and *Eucinostomus argenteus* also dominating.

From this discussion it can be seen that the species richness of the larval and juvenile assemblages of the mangrove and seagrass are

relatively similar. In addition, similarities in composition are evident between the mangrove and seagrass assemblages of each life-stage. However, the adults show a marked drop in species richness from the mangrove to the seagrass habitat, and only have one of the predominant species in common. In order to elucidate whether individual species are obligate or facultative residents of either habitat, a comparison of the larval, juvenile and adult assemblages within and between the mangrove and seagrass habitats is required.

Key points

The key findings discussed here may be summarised as:

- 159 species or types from 50 families were recorded from the mangroves and seagrass of Calabash Cay;
- larval stages of 120 species or types in 44 families were identified;
- juveniles of 50 species or types in 20 families were identified;
- adults of 36 species or types in 19 families were recorded.

3.2.2 Comparison of species and family composition of life-stages within and between habitats

In the surveys of the mangroves and seagrass, only 7 and 9 taxa respectively were recorded as both larvae and juveniles (Appendix 3.1). Although some error will be due to identification to different taxonomic levels, this is unlikely to account for all the species or types present as larvae but not as juveniles in the mangroves and seagrass, which number 63 and 80 respectively. Of those present at both stages, *Atherinomorus stipes*, *Strongylura notata*, *Chaetodon* sp. and Clupeidae Type A were recorded from the mangrove habitat, while *Thalassoma bifasciatum*, *Ocyurus chrysurus*, *Monacanthus* sp., Pomacentridae Type A, *Scarus* sp. and *Hypoplectrus unicolor* were present in the seagrass. *Halichoeres* sp., *Sparisoma* sp. and *Sphyraena barracuda* were recorded from both habitats, and were also present as adults in both habitats.

All three life stages of *Atherinomorus stipes* and *Chaetodon* sp. were recorded from the mangroves, and *Ocyurus chrysurus*, *Scarus* sp. and *Hypoplectrus unicolor* from the seagrass beds. None of these are restricted to a single habitat, however, when considering all three life stages. Larvae of *A.stipes* were also recorded from the seagrass habitat, as were juveniles and adults of the genus *Chaetodon*. Similarly, juvenile and adult phases of *O.chrysurus*, *Scarus* sp. and *H.unicolor* were recorded from the mangrove habitat.

Three additional species, *Cryptotomus roseus*, *Eucinostomus jonesi* and *Strongylura notata*, were recorded at all three life stages, but across both habitats. Juveniles and adults of *C.roseus* were present in the mangroves, with larvae and adults in the seagrass. Larvae and adults of *E.jonesi* were found in the mangroves, with juveniles and adults recorded from the seagrass. *S.notata* was present as larvae and juveniles in the mangroves, and as larvae and adults in the seagrass beds. Therefore all three life stages of 12 species or types were recorded across both habitats.

The drop in species numbers between successive life stages may not only be due to a physical loss of larvae. Some species are small and/or cryptic as juveniles and adults, and as a result not easily detected by visual census surveys. Species that school as juveniles and adults are present in high numbers, but have a very narrow range of distribution for individual shoals, that may fall outside the transects covered by visual census surveys.

Of the larval taxa recorded solely from the mangrove habitat, 29 out of a total of 31 were not present as juveniles or adults in either habitat. All 29 can be rated as rare species, as their relative abundance ranged from 0.13 to 0.94 %, each constituting 1 % or less of the total mangrove larval assemblage. Each of these species or types appears to

have an obligate dependency on the mangrove habitat as a nursery ground, but may occupy habitats other than the mangroves or seagrass as adults and juveniles.

Of the 18 that could be identified to genus or species level, many are difficult to detect as adults or juveniles. Among these were 5 gobies (Gobiidae), 3 blennies (Blennioidei), 2 pipefish (Syngnathidae), 2 eels (Ophichthidae, Ophidiidae) and an eleotrid (Eleotridae), all of which are small and generally cryptic as juveniles and adults. The genus *Astrapogon* was also recorded, adults of which usually inhabit invertebrate shells during daylight. Two scarid species recorded, *Scarus coeruleus* and *Sparisoma chrysopterum*, may have been present as juveniles or adults but most scarids at these stages could only be identified to genus level. Both genera were present as juveniles and adults in both habitats. The remaining two species, *Anchoa cayorum* and *Joturus pilchardi*, both occur in large schools at later life stages.

In the seagrass habitat, 28 of the larval taxa recorded solely from there were not present as juveniles or adults in either habitat. Their relative abundance ranged from 0.05 to 0.47 %, each constituting 0.5 % or less of the total seagrass larval assemblage. Again, not all could be identified to species or genus, with the result that only 21 will be considered. Of these there were 4 blennies, 1 goby, 1 pipefish, 1 eel (Muraenidae), 1 pearlfish (Carapidae) and 1 frogfish (Antenariidae), all cryptic as juveniles and adults. The species *Albula vulpes*, *Oligoplites saurus*, *Harengula* sp., *Elops saurus* and *Megalops atlanticus* occur in large schools at subsequent life stages. *Diapterus auratus*, *Holocanthus tricolor*, *Stegastes* sp. and *Synodus* sp. may have been present in the mangroves, or as older life stages, as types of their respective families were recorded that may have been the same genus or species. As in the mangroves, the 2 scarid species identified, *Scarus iserti* and *Sparisoma radians*, may have been present as juveniles or

adults but most scarids at these stages could only be identified to genus level.

Most larvae are omnivorous initially, with a mixed diet consisting of a wide range of phytoplankton and zooplankton, and may not specialise until reaching the juvenile stage. Any niche partitioning of larval species as a result of diet is only possible if stomach contents are identified to a high taxonomic level, which is lacking in the present study. The same is not true for juvenile and adult species, the diets of which vary more in general type. Consequently, niche partitioning according to general feeding guilds of those families present as juveniles and/or adults can be estimated (Table 3.2).

Table 3.2. The general feeding guilds of families recorded as juveniles and/or adults by visual census surveys. General carnivores have a diet consisting either solely of invertebrates, or of fish and invertebrates.

Herbivore	Zooplanktivore	General carnivore	Piscivore	Omnivore
Acanthuridae	Atherinidae	Diodontidae	Belonidae	Balistidae
Scaridae	Clupeidae	Gerreidae	Carangidae	Chaetodontidae
	Gobiidae	Haemulidae	Sphyraenidae	Monacanthidae
		Labridae		Ostraciidae
		Lutjanidae		Pomacanthidae
		Mullidae		Pomacentridae
		Ophidiidae		
		Sciaenidae		
		Serranidae		
		Sparidae		
		Tetraodontidae		
		Urolophidae		

Six species or types of fish were present only as juveniles in the mangrove habitat: *Acanthurus coeruleus*, Balistidae Type A, *Lutjanus analis*, *Lutjanus cyanopterus*, *Lutjanus jocu* and *Pomacanthus paru*. All had a relative abundance of less than 0.5 % with the exception of *L.jocu*, which constituted 2.19 % of the mangrove juvenile assemblage. By contrast, 13 species or types were recorded only as juveniles in the seagrass habitat, all with a relative abundance between 0.11 and 0.77 %. Of these, the genera *Diodon* sp. and *Haemulon* sp., and the type

Mullidae Type A, may not be representative of separate species, as species of the same genera and families were identified; *Diodon holocanthus, Haemulon chrysargyreum, Haemulon melanorum, Haemulon parra* and *Pseudupeneus maculatus*. The remaining five species or types present were *Caranx bartholomaei, Chaetodon ocellatus, Eucinostomus melanopterus, Bodianus rufus* and Tetraodontidae Type A.

Only a single type was present solely as an adult in the mangrove habitat, the boxfish Ostraciidae Type A, with a very low relative abundance of 0.09 %. Boxfishes are territorial and solitary, and therefore only likely to be present in low numbers. Of the two species present solely in the seagrass, Carangidae Type A and *Urobatis jamaicensis*, the latter is also solitary. Both have low relative abundances, 0.63 and 0.31 % respectively.

Consideration of the distribution of juvenile and adult species within feeding guilds across the habitats gives little indication of any habitat preference according to food availability, with the exception of zooplanktivores, which appear to have a higher relative abundance in the mangrove habitat (Figure 3.3). However, this is due mainly to large shoals of juvenile and adult *Atherinomorus stipes* in the mangroves, compared with adult gobies in both habitats, which are usually solitary, or in pairs. Examination of the larval distribution shows that *A.stipes* larvae are also present in the seagrass habitat.

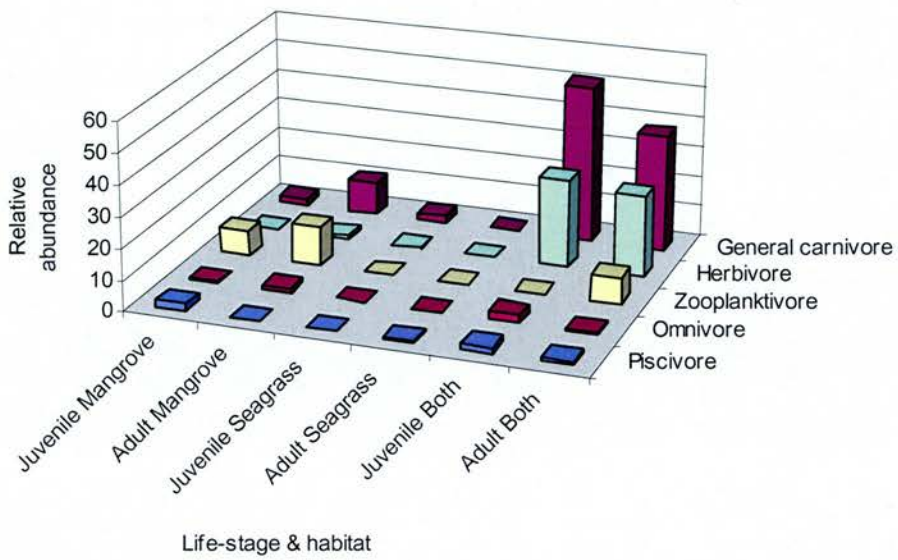


Figure 3.3. Relative abundance of juveniles and adults according to 5 feeding guilds. Abundance is calculated as the percentage of the total juvenile or adult assemblage respectively, and divided into those present solely in the mangrove or seagrass at the juvenile or adult stage, or in both habitats (i.e. juveniles total 100 %, adults total 100 %). The predominant feeding guild for both stages is the general carnivore, across both habitats, which takes a mixture of invertebrates and fish. Herbivores also have a relatively high abundance and show a similar distribution across both habitats.

Based on their sole presence in the respective habitats, 41 taxa appear to have an obligate dependency on mangroves during one or more stages of their life cycle. Similarly, 46 taxa are apparently obligate dependents on the seagrass beds. However, this is based on comparison across all life stages, and only 12 species or types were recorded at all stages. Of these, none showed an obligate dependency on either the mangrove or the seagrass habitat throughout their life cycle.

Key points

The key findings discussed here may be summarised as:

- 41 taxa from 26 families were recorded solely from the mangrove habitat, at one (or more) life stage(s);
- 46 taxa from 29 families were recorded solely from the seagrass habitat, at one (or more) life stage(s);

- of the species or types present at all three life stages, none were confined to a single habitat;
- all three life stages of *Halichoeres* sp., *Sparisoma* sp. and *Sphyraena barracuda* were recorded in both habitats;
- the predominant feeding guilds of juveniles and adults are herbivore and general carnivore, and are relatively evenly distributed across both habitats.

3.3 *Discussion*

The taxa recorded from the mangroves and seagrass of Calabash Cay totalled 159 species from 50 families. This compares relatively well with the total of 205 species from 54 families previously recorded for the coral reefs of the Turneffe Islands atoll (Harborne, 2000), and 87 species from 34 families reported from a shallow lagoon in northern Belize (Sedberry & Carter, 1993). When divided into the component life stages, the number of taxa decreased from the larval to the juvenile to the adult stages, with 120, 50 and 36 taxa respectively. Both larvae and juveniles may be lost through migration between habitats, as well as through predation, starvation and disease.

The larval assemblage in the mangroves was dominated by *Hypoplectrus* sp., a mainly carnivorous genus of some value as an aquarium fish. The zooplanktivore *Atherinomorus stipes*, of limited value as bait, dominated the seagrass larval assemblage, and was also abundant in the mangrove larval, juvenile and adult assemblages. Atherinids have dominated assemblages in similar studies (Thayer *et al.*, 1987; Boulon, 1992; Dennis, 1992; Sponaugle & Cowen, 1996; Ley *et al.*, 1999), but are small fish that occur in large schools, and therefore will always occur in high densities.

The juvenile mangrove assemblage was dominated by *Haemulon flavolineatum*, a species of commercial fisheries value commonly found in mangrove habitat (Dennis, 1992; Claro & Garcia-Arteaga,

1993; Sedberry & Carter, 1993). The carnivorous *Lutjanus apodus* and *Lutjanus griseus* are also relatively abundant in the mangrove habitat compared to the seagrass as juveniles and adults, and are both distinctive mangrove predators. The most abundant juvenile, and adult, in the seagrass was *Scarus* sp., a herbivore of limited fisheries value. Although *A.stipes* was the most abundant adult in the mangroves, *Haemulon sciurus*, a relatively large fish of minor commercial fisheries value, also had a high abundance.

Approximately a quarter of the taxa were recorded only from the mangrove habitat, and another quarter solely from the seagrass beds (41 and 46 taxa from 26 and 29 families respectively). Initially these figures suggest that half of the taxa recorded had an obligate dependency on either the mangroves or the seagrass at one or more of their life stages. However, many were recorded in low proportions, constituting less than 1 % of the respective larval, juvenile or adult assemblage of either habitat. Consequently, their definition as obligate mangrove or seagrass residents should not be treated as steadfast. This is particularly so because many were not observed at all life stages, and therefore are probably only obligate users at individual stages. Of the 8 taxa present at all three life stages, none were confined to a single habitat.

Although all three life stages of *Halichoeres* sp., *Sparisoma* sp. and *Sphyraena barracuda* were recorded in both habitats, they show marked differences in ecology. The labrid *Halichoeres* sp. tends to be a generalised carnivore and is of some value as a food fish and in aquaria. The herbivorous scarid *Sparisoma* sp. is also of some value in artisanal fisheries. Despite their differences in diet, the two genera are often observed together in mixed shoals. *Sphyraena barracuda* is a predator, in particular of fishes, and is an established resident of mangrove and seagrass habitats in its larval and juvenile stages (De Sylva, 1963). Generally solitary, it is of value in minor commercial

fisheries and show aquaria, and of particular importance as a gamefish with a maximum size of 2 metres.

The more abundant labrids and scarids belong to the two feeding guilds with the greatest relative abundance in both habitats, the herbivores and the carnivores. The soft-bottom of the mangrove habitat and seagrass beds is likely to have a high density of benthic invertebrates for the general carnivores, while algae on mangrove prop-roots and the seagrass plants provide an extensive food source for herbivores. For zooplanktivores, planktonic feeding may not be very efficient in the sheltered environment of the mangroves and seagrass beds. Many of the omnivorous taxa are solitary and cryptic, and therefore likely to be poorly represented in visual census surveys. The piscivores are also solitary and from the nature of their position at the top of the food web only present in low numbers.

The high proportion of species with a facultative dependency on both mangrove and seagrass habitats may reflect the fact that there appears to be little difference in general food type availability between the two habitats. Of those that do appear to be obligate residents of either habitat, all represent a low proportion of the entire fish assemblage, suggesting that specialised diets may be a factor in their distribution. The main difference between the habitats is likely to be in their structure, reflecting in turn the amount of shelter available for and from predators. Shelter and predation pressure are likely to be more influential in determining species distribution, and the relationship between habitat structure and assemblage composition merits further examination.

The next chapter discusses the dynamics of the physical environment around Calabash Cay, and its influence on the spatial and temporal distributions of reef fish.

Appendix 3.1. The relative abundance (%) of larval (L), juvenile (J) and adult (A) stages of fish species recorded from the mangrove and seagrass habitats of Calabash Cay, calculated separately for each stage within each habitat.

Family / order	Species / type	Mangrove			Seagrass		
		L	J	A	L	J	A
Acanthuridae	*Acanthurus bahianus* Castelnau, 1855			0.27		0.11	
	Acanthurus chirurgus (Bloch, 1787)		0.33	0.53		0.11	
	Acanthurus coeruleus Bloch & Scneider, 1801		0.14				
	Acanthurus sp		2.00	1.16		4.04	
Achiridae	*Achirus lineatus* (Linnaeus, 1758)	0.40			0.05		
Albulidae	*Albula vulpes* (Linnaeus, 1758)				0.21		
Antenariidae	*Histrio histrio* (Linnaeus, 1758)				0.05		
Apogonidae	*Apogon* sp	0.13			0.05		
	Astrapogon sp	0.13					
Atherinidae	*Atherinomorus stipes* (Müller & Troschel, 1848)	11.8	12.6	25.1	23.0		
Balistidae	Balistidae Type A		0.09				
Belonidae	*Strongylura notata* (Poey, 1860)	0.27	4.19		0.05		0.31
	Belonidae Type A				0.05		
Blenniidae	*Parablennius marmoreus* (Poey, 1876)				0.05		
Blennioidei	Blennioidei Type A	0.4			0.79		
	Blennioidei Type B	1.47			1.47		
	Blennioidei Type C	0.13			4.66		
	Blennioidei Type D	4.02			14.2		
	Blennioidei Type E	1.47			4.87		
	Blennioidei Type F	2.41			3.14		
	Blennioidei Type G	0.13			0.05		
	Blennioidei Type H				0.10		
	Blennioidei Type I				0.05		
	Blennioidei Type J				0.16		
	Blennioidei Type K				0.05		
	Blennioidei Type L				0.05		
	Blennioidei Type M	0.13					
	Blennioidei Type N	0.13					
Carangidae	*Caranx bartholomaei* Cuvier, 1833					0.33	
	Oligoplites saurus (Bloch & Schneider, 1801)				0.05		
	Carangidae Type A						0.63
Carapidae	*Carapus bermudensis* (Jones, 1874)				0.47		
Chaenopsidae	*Acanthemblemaria chaplini* Böhlke, 1957	0.54					
	Stathmonotus stahli tekla (Evermann & Marsh, 1899)	0.13					
	Chaenopsidae Type A	0.27					
Chaetodontidae	*Chaetodon capistratus* Linnaeus, 1758		1.49	0.98		0.11	0.31
	Chaetodon ocellatus Bloch, 1787					0.22	
	Chaetodon sp	0.13	0.14	0.62			
Clupeidae	*Brevoortia* sp	2.14			1.89		
	Harengula sp				0.47		
	Jenkinsia lamprotaenia (Gosse, 1851)	2.28			1.26		
	Jenkinsia parvula Cervigón & Velasquez, 1978	5.50			3.20		
	Sardinella aurita Valenciennes, 1847	0.94			1.36		
	Clupeidae Type A	5.09	3.72		1.89		
	Clupeidae Type B				0.05		
Clupeiformes	Clupeiformes Type A	0.13					
Dactyloscopidae	*Gillellus jacksoni* Dawson, 1982				0.05		
	Gillellus uranidae Böhlke, 1968				0.26		
Diodontidae	*Diodon holocanthus* Linnaeus, 1758					0.11	
	Diodon sp					0.22	

Family / order	Species / type	Mangrove			Seagrass		
		L	J	A	L	J	A
Eleotridae	*Eleotris* sp	0.27					
Elopidae	*Elops saurus* Linnaeus, 1766				0.05		
Engraulidae	*Anchoa cayorum* (Fowler, 1906)	0.13					
	Anchoa lamprotaenia Hildebrand, 1943	0.40			0.94		
	Anchoviella perfasciata (Poey, 1860)	0.67			2.20		
	Lycengraulis grossidens (Agassiz, 1829)	0.40			1.05		
	Engraulidae Type A				0.10		
Exocoetidae	Exocoetidae Type A	0.13					
Gerreidae	*Diapterus auratus* Ranzani, 1842				0.05		
	Diapterus rhombeus (Cuvier, 1829)	0.13			0.10		
	Eucinostomus argenteus (Baird & Girard, 1855)		0.98	1.33		4.59	4.72
	Eucinostomus jonesi (Günther, 1879)	0.13		0.09		1.20	0.63
	Eucinostomus lefroyi (Goode, 1874)	3.08			1.62		
	Eucinostomus melanopterus (Bleeker, 1863)					0.11	
	Eugerres plumieri (Cuvier, 1830)	0.27			0.05		
	Gerres cinereus (Walbaum, 1792)		2.65	0.27		1.20	0.63
	Gerreidae Type A		1.44	0.09			
Gobiesocidae	*Gobiesox punctulatus* (Poey, 1876)	6.43			2.83		
Gobiidae	*Bathygobius curacao* (Metzelaar, 1919)	5.23			1.57		
	Bathygobius soporator (Valenciennes, 1837)	0.13					
	Bathygobius sp	0.27			0.31		
	Coryphopterus glaucofraenum Gill, 1863	0.27					
	Coryphopterus sp	1.07			2.10		
	Evorthodus lyricus (Girard, 1858)	2.14			0.21		
	Gnatholepis thompsoni Jordan, 1904	0.13					
	Gobionellus boleosoma (Jordan & Gilbert, 1882)	0.13					
	Gobionellus saepepallens Gilbert & Randall, 1968	2.01			1.10		
	Gobionellus sp	0.27					
	Gobiosoma bosci (Lacepède, 1800)				0.21		
	Gobiosoma sp	4.02			1.31		
	Microgobius gulosa (Girard, 1858)	0.13			0.05		
	Nes longus (Nichols, 1914)	0.27			0.26		
	Gobiidae Type A	0.13		0.62	0.10		16.4
	Gobiidae Type B	0.13			0.10		
	Gobiidae Type C				0.05		
	Gobiidae Type D				0.05		
	Gobiidae Type E	0.13					
	Gobiidae Type F	0.13					
Haemulidae	*Anisotremus virginicus* (Linnaeus, 1758)		0.14	0.09			
	Haemulon chrysargyreum Günther, 1859					0.66	
	Haemulon flavolineatum (Desmarest, 1823)		34.1	8.81		8.96	
	Haemulon melanorum (Linnaeus, 1758)					0.11	
	Haemulon parra (Desmarest, 1823)					0.66	
	Haemulon plumieri (Lacepède, 1801)		0.09	1.07			1.57
	Haemulon sciurus (Shaw, 1803)		3.26	17.4		8.42	2.52
	Haemulon sp					0.11	
	Haemulidae Type A	0.13			0.10		
Labridae	*Bodianus rufus* (Linnaeus, 1758)					0.55	
	Doratonotus megalepis Günther, 1862	0.40		0.18	0.42		
	Halichoeres sp	0.13	0.33	3.65	0.05	15.6	21.1
	Thalassoma bifasciatum (Bloch, 1791)		0.05		0.05	0.22	
	Xyrichtys sp				0.16		
	Labridae Type A	0.27					
Labrisomidae	*Malacoctenus gilli* (Steindachner, 1867)				0.16		
	Malacotenus sp	0.13			2.20		
	Starksia starcki Gilbert, 1971	0.13					
	Labrisomidae Type A	0.13			0.16		
Lutjanidae	*Lutjanus analis* (Cuvier, 1828)		0.37				
	Lutjanus apodus (Walbaum, 1792)		10.4	11.6		0.11	
	Lutjanus cyanopterus (Cuvier, 1828)		0.47				
	Lutjanus griseus (Linnaeus, 1758)		6.75	12.6		0.44	3.77
	Lutjanus jocu (Bloch & Schneider, 1801)		2.19				
	Lutjanus mahogoni (Cuvier, 1828)		0.37	0.27		0.11	
	Ocyurus chrysurus (Bloch, 1791)		0.09	0.09	0.21	2.73	3.46

Family / order	Species / type	Mangrove			Seagrass		
		L	J	A	L	J	A
Megalopidae	*Megalops atlanticus* Valenciennes, 1847				0.05		
Monacanthidae	*Monacanthus setifer* Bennett, 1831	0.13			1.83		
	Monacanthus sp	0.54			0.84	0.11	
Mugilidae	*Joturus pilchardi* Poey, 1860	0.13					
	Mugilidae Type A				0.05		
Mullidae	*Pseudupeneus maculatus* (Bloch, 1793)					0.77	
	Mullidae Type A					0.11	
Muraenidae	*Gymnothorax moringa* (Cuvier, 1829)				0.05		
Ophichthidae	*Myrophis punctatus* Lütken, 1851	0.13					
Ophidiidae	*Ophidion* sp	0.13					
Ostraciidae	Ostraciidae Type A			0.09			
Pomacanthidae	*Holacanthus tricolor* (Bloch, 1795)				0.05		
	Pomacanthus arcuatus (Linnaeus, 1758)			0.27	0.05		
	Pomacanthus paru (Bloch, 1787)		0.05				
	Pomacanthidae Type A	2.95			3.25		
Pomacentridae	*Abudefduf saxatilis* (Linnaeus, 1758)		2.09	0.71		0.44	
	Stegastes diencaeus (Jordan & Rutter, 1897)	0.13			0.21		
	Stegastes sp				0.05		
	Pomacentridae Type A		0.28	0.53	0.05	0.66	
Scaridae	*Cryptotomus roseus* Cope, 1871		0.09	0.09	0.21		0.31
	Scarus coeruleus (Bloch, 1786)	0.13					
	Scarus iserti (Bloch, 1789)				0.26		
	Scarus sp		6.10	8.54	0.47	41.5	30.2
	Sparisom chrysopterum (Bloch & Schneider, 1801)	0.27					
	Sparisoma radians (Valenciennes, 1840)				0.05		
	Sparisoma sp	0.54	0.19	2.05	1.36	3.28	11.0
Sciaenidae	Sciaenidae Type A			0.18	0.26		
Scorpaenidae	*Scorpaena* sp	0.27			0.42		
Serranidae	*Epinephelus striatus* (Bloch, 1792)		0.05	0.09			
	Hypoplectrus sp	21.0			4.45		
	Hypoplectrus unicolor (Walbaum, 1792)		0.05	0.09	0.42	0.87	0.63
Sparidae	*Archosargus probatocephalus* (Walbaum, 1792)			0.09			
	Sparidae Type A	0.40					
Sphyraenidae	*Sphyraena barracuda* (Walbaum, 1792)	0.13	2.79	0.44	0.05	0.98	1.57
Syngnathidae	*Bryx dunckeri* (Metzelaar, 1919)				0.10		
	Bryx randalli (Herald, 1965)	0.13					
	Cosmocampus bracycephalus (Poey, 1868)	0.13					
	Syngnathidae Type A	1.21			1.00		
	Syngnathidae Type B	0.94					
Synodontidae	*Synodus* sp				0.05		
	Synodontidae Type A	0.13					
Tetraodontidae	*Sphoeroides maculatus* (Bloch & Schneider, 1801)	0.13			0.26		
	Tetraodontidae Type A					0.22	
Tripterygiidae	Tripterygiidae Type A	0.13			0.05		
Urolophidae	*Urobatis jamaicensis* (Cuvier, 1816)						0.31

4.0 Spatio-temporal variation of reef fish abundance with environmental variables in the mangrove and seagrass habitats of a Caribbean island

4.1. *Introduction*

The linkages of fishes between shallow water biotopes remain largely unknown, as studies have generally been conducted within single biotopes (Pollard, 1984; Thayer *et al.*, 1987; Doherty & Williams, 1988; Parrish, 1989; Dennis, 1992; van der Velde *et al.*, 1992). Of those studies in which two or more habitats have been compared, different methodologies have often been used due to the differences in habitat structure, making comparisons difficult. The use of a single methodology to survey various habitats has been shown to be important in the assessment of their function (Sedberry & Carter, 1993; Nagelkerken *et al.*, 2000b).

Mangroves and seagrass beds are considered nurseries to numerous reef fish species in the Caribbean, Western Atlantic and Indo-Pacific Ocean (Pollard, 1984; Parrish, 1989). The benefits of such habitats to the early life history stages of reef fish has been explained in terms of shelter against predators, low predator abundance, high interception rate of vegetation to planktonic larvae and high food availability (Odum & Heald, 1972; Blaber & Blaber, 1980; Orth *et al.*, 1984; Parrish, 1989; Nagelkerken, 2000). Spatial separation of size-classes between different habitats suggests movement from one habitat to another during life-cycle stages, and such migration has been inferred for many fish species, with larger individuals found progressively offshore (Yàñez-Arancibia *et al.*, 1988; Cocheret de la Morinière *et al.*, in press).

Possible physical mechanisms instigating or promoting migration from within and between habitats are environmental variables such as water temperature, extinction coefficient, turbidity, sulphate and nitrate ion concentration, salinity, pH and wind velocity, or gradients and seasonal changes therein, and habitat structural parameters in particular habitat complexity. Understanding the underlying processes affecting survival and therefore recruitment is increased by establishing which factors are most influential in determining the spatial and temporal distributions of early life stages within and between shallow-water habitats.

The nested spatial design of the present study, as described in *Chapter 2*, enables analysis of the different life stages and physical variables on scales of 10s, 100s and 1000s of metres. The habitat structural parameters are assumed to vary on a spatial but not on a temporal scale. The environmental variables measured during the larval collection vary with both space and time, and therefore have a potential influence on the temporal as well as the spatial distribution patterns of the larvae. Any general spatial patterns evident in the environmental variables may also influence the distribution of the juvenile and adult assemblages.

The research questions addressed are:

1. Do the larval, juvenile and adult life stages of reef fish display any preference for mangrove or seagrass habitats?
2. Within each habitat, are the density and size distribution of the larval, juvenile and adult assemblages influenced by variation in the habitat structure and other environmental variables?
3. How influential is the temporal variation in environmental factors on the temporal patterns of larval density and size distribution in the mangrove and seagrass habitats?

4.2. *Results*

4.2.1. Habitat preference of larval, juvenile and adult life stages

The monospecific mangrove habitat of Calabash Cay consists of *Rhizophora mangle*, with prop-roots that reach several metres in length, and grow densely to form almost solid walls (Figure 4.1). The surrounding seagrass beds consist predominantly of *Thalassia testudinum*, a broad-leafed species growing up to a metre in height, often very dense.

The mean density of the larval assemblage is lower in the mangroves than in the seagrass, significantly so during the day but not at night (Table 4.1). The opposite trend is evident in the juvenile and adult assemblages, both of which have significantly higher densities in the mangroves than in the seagrass beds. However, the mean body size of each life history stage is significantly smaller in the seagrass than in the mangroves.

Table 4.1. Mean density and size (total body length) ± standard error of each life stage, in the mangrove and seagrass habitats. Mean sizes are in cm, densities are in the specific sampling unit of the individual method used: larvae per light trap at night, larvae per 100 m^3 plankton net tow during daylight, juveniles and adults per 30 m^3 transect. All mangrove/seagrass pairs of values differ significantly ($p < 0.05$) unless marked by *.

	Density		Size (cm)	
	Mangrove	**Seagrass**	**Mangrove**	**Seagrass**
Larva	*2.45 (0.35) / trap	*3.34 (0.77) / trap	0.75 (0.02)	0.64 (0.02)
	0.47 (0.07) / $100m^3$	3.06 (0.55) / $100m^3$		
Juvenile	45.72 (7.03) / $30m^3$	20.80 (2.20) / $30m^3$	9.15 (0.11)	5.98 (0.13)
Adult	23.42 (3.76) / $30m^3$	6.63 (1.13) / $30m^3$	14.58 (0.22)	12.93 (0.56)

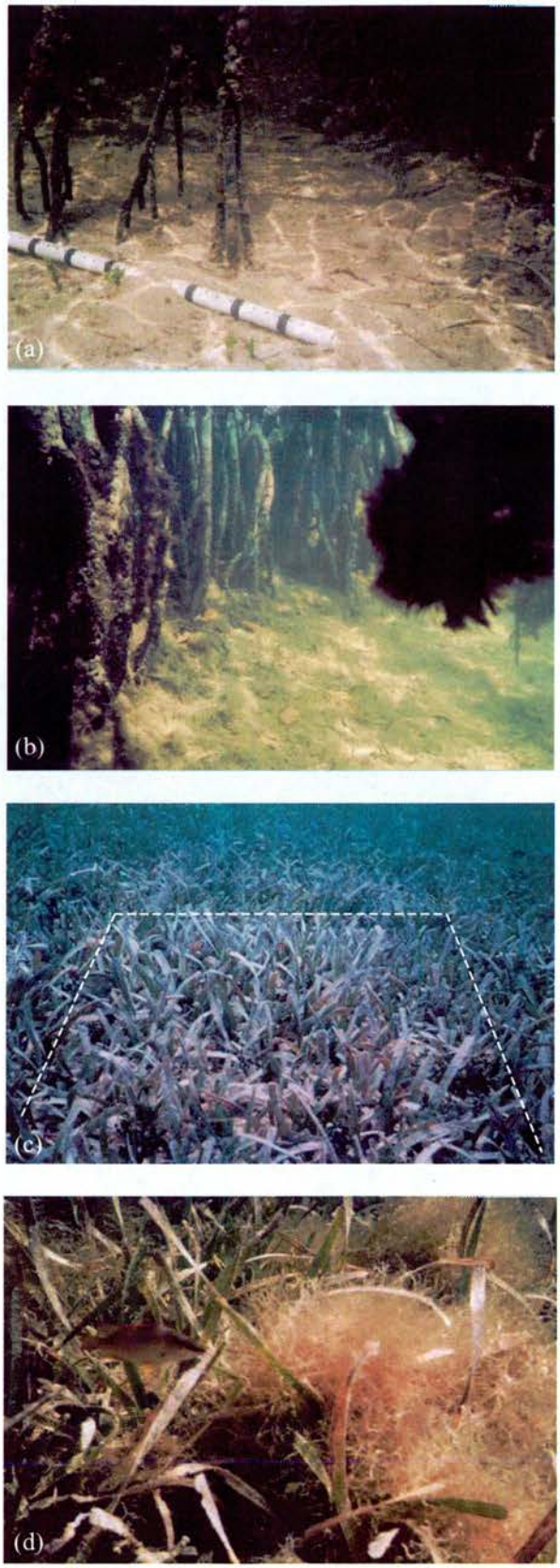


Figure 4.1. Examples of the mangrove prop-root (a, b) and seagrass (c, d) habitats of Calabash Cay. In (a) a pipe marked off in 10 cm intervals lies at the outer edge of a *Rhizophora mangle* stand. In (c) a 1 m^2 quadrat of *Thalassia testudinum* is indicated by a dotted outline.

Smaller size classes represent a greater proportion of the larval assemblage, in particular in the seagrass beds (Figure 4.2). In both habitats, the smallest three size classes have significantly higher abundances than the remainder (ANOVA: $F = 38.78$, $p \leq 0.001$; $F = 67.78$, $p \leq 0.001$). In the smallest size class of < 0.5 cm body length, the abundance of larvae in the seagrass is significantly higher than that in the mangroves (Two-sample T-test: $T = -3.38$, $p \leq 0.001$). The greatest percentages of larvae are in the same size class, and therefore only a few days old.

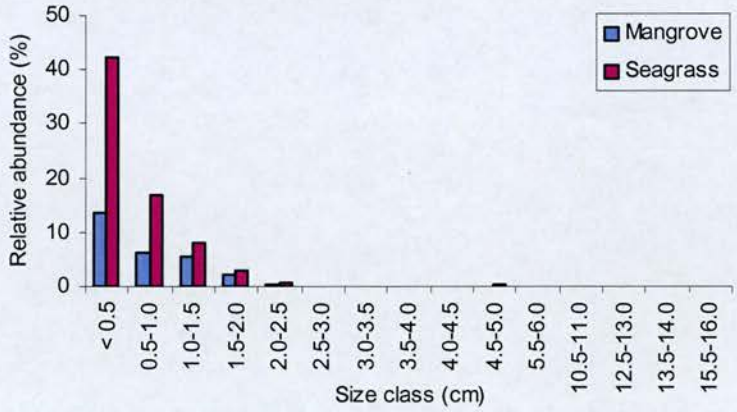


Figure 4.2. Relative abundance (%) of larvae in standard length size classes, of 0.5 cm increments, calculated as a percentage of the entire larval assemblage. Size classes of over 6 cm relate solely to *Carapus bermudensis*, a commensal species of the pearlfish. The smaller size classes account for the greater proportion of larvae, especially in the seagrass beds. The greatest percentages of larvae are in the size class of ≤ 0.5 cm in length, and only a few days old.

In the juvenile assemblage, the greatest proportion is represented by the smaller sizes of < 15 cm in the mangroves and < 10 cm in the seagrass beds (Figure 4.3). The smallest three size classes have significantly higher abundances than the remainder in both habitats (ANOVA: $F = 52.61$, $p \leq 0.001$; $F = 105.29$, $p \leq 0.001$). In the first size class of < 5 cm, the relative abundance of juveniles is very similar in the two habitats, while in the next three size classes of 5 cm increments, the relative abundance in the mangroves is significantly greater than that in the seagrass (Two-sample T-test: $T = 2.14$, $p = 0.035$; $T = 8.97$, $p \leq 0.001$; $T = 5.09$, $p \leq 0.001$).

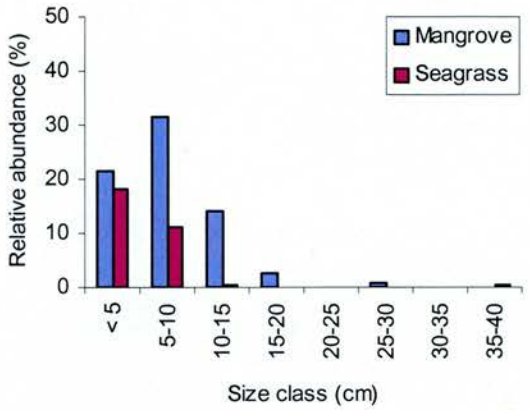


Figure 4.3. Relative abundance (%) of juvenile fish in standard length size classes of 5 cm increments. Calculated as a percentage of the entire juvenile assemblage. In the mangroves the majority of juveniles are ≤ 10 cm in length, while in the seagrass the greatest proportion are ≤ 5 cm.

The adult assemblage in the mangrove habitat shows a relatively even distribution between the first four size classes (Figure 4.4). However, the relative abundance of adults in the second, third and fourth size classes, covering 5 – 20 cm body length, is significantly greater than in the remaining size classes, including the smallest of < 5 cm (ANOVA: $F = 26.98$, $p \leq 0.001$).

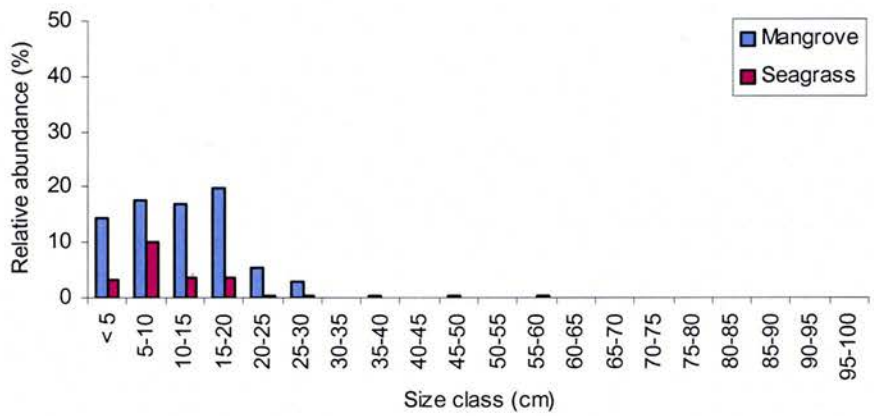


Figure 4.4. Relative abundance (%) of adult fish in standard length size classes of 5 cm increments. Calculated as a percentage of the entire adult assemblage. In the mangroves the majority of adults are ≤ 20 cm in length, while in the seagrass the greatest proportion are ≤ 10 cm.

In the seagrass beds, the relative abundance of adults in the 5 – 10 cm size class is significantly greater than in the remaining classes (ANOVA: $F = 25.13$, $p \leq 0.001$). The first and third size classes in turn both have a significantly higher relative abundance of adults than the

remaining classes with the exception of 15 – 20 cm. The relative abundance of adults in the mangroves consistently exceeds that in the seagrass across all the size classes, differing significantly for the intermediate size classes covering 10 – 30 cm (Two-sample T-test: $T = \geq 3.28$, $p \leq 0.001$).

Overall, all three life stages display a habitat preference in terms of their total abundance, and the relative abundance of size classes. Reef fish larvae exhibit a preference for seagrass, while the juveniles and adults prefer the mangrove prop-root habitat. There appears to be habitat partitioning according to body size for each life stage, with a greater abundance of the smaller larvae present in the seagrass beds than the mangroves, while the smaller individuals of the juveniles and adults are predominant in the mangrove habitat.

Key points

The key points of the habitat preference of larval, juvenile and adult fish may be summarised as:

- mean body size of each life history stage is significantly smaller in the seagrass than in the mangroves;
- larval density is significantly lower in the mangroves than the seagrass during the day, while no significant difference is apparent at night;
- both juveniles and adults have significantly higher abundance in the mangroves than in the seagrass;
- a greater proportion of the larval assemblage is represented by smaller sizes of 0 – 1.5 cm, in particular in the seagrass habitat;
- a greater proportion of the juvenile assemblage is represented by smaller sizes of 0 – 15 cm, in particular in the mangrove habitat;
- a greater proportion of the adult assemblage is represented by smaller sizes of 5 – 20 cm, in particular in the mangrove habitat.

4.2.2. Spatial variation of abiotic variables and fish assemblages within each habitat

The differences in the abundance of the three life stages suggest that as general habitat types, the seagrass is more suitable for smaller and earlier stages, while mangrove prop-roots are preferable for larger and later stages. The suitability of either habitat may be due to its structural complexity or to other environmental variables. In the mangrove habitat, the structural parameters deemed to be of importance are the water depth, the prop-root density and length, and the length of prop-roots relative to the water depth. The equivalent structural features measured in the seagrass beds are the water depth, percent seagrass cover, and the leaf height and density. All the parameters vary spatially, and with the exception of the water depth were measured once. The additional environmental variables considered to be of importance are water temperature, light intensity, wind speed, pH, salinity, turbidity, nitrate ion and sulphate ion levels. All these physical parameters vary with time as well as space, and were measured during each plankton-net survey. As temporal variation in water depth occurs due to tidal cycles, measurements were taken during each set of larval collections or visual census surveys.

Habitat parameters and fish densities

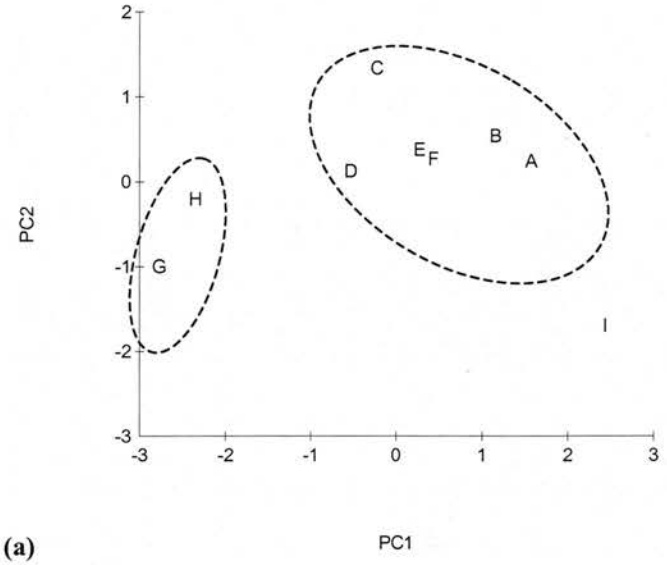
Although the habitat structure parameters of the mangroves and seagrass are analogous, they cannot be compared directly. Within each habitat, spatial variation according to Regions is evident (Table 4.2). A clear trend of changing habitat structure with Station as well as Region is apparent for both habitats (Figure 4.5). Both mangrove and seagrass differ significantly in structural parameters between Regions, but not between Stations nested within Regions (2-way nested ANOSIM: $R = 0.227$, $p \leq 0.001$; $R = 0.377$, $p \leq 0.001$; $R = 0.235$, $p = 0.093$; $R = 0.300$, $p = 0.061$ respectively).

Table 4.2. Mean values ± standard error of habitat structure parameters measured in the mangrove and seagrass habitats of Regions 1, 2 and 3. The symbol † indicates a significantly different mean ($p < 0.05$). In the mangroves the mean water depth and prop-root length of Region 1 are both significantly lower than in Regions 2 and 3. In the seagrass the mean water depth of Region 2 is significantly greater than in Regions 1 and 3.

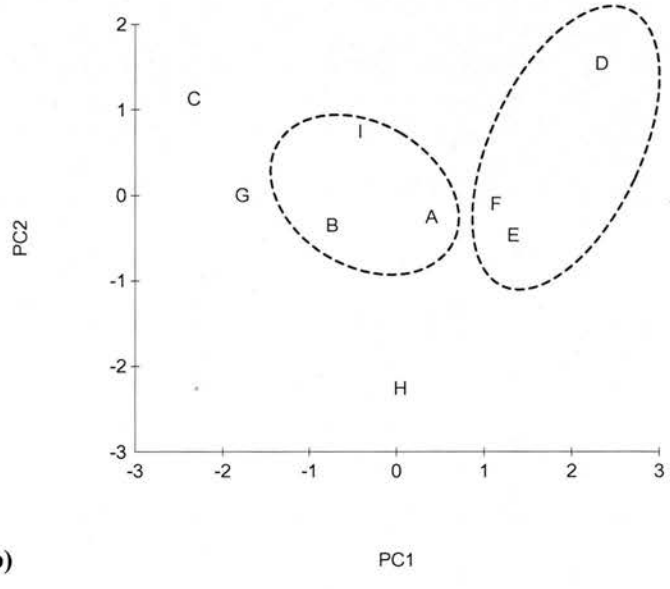
	Regions		
	1	2	3
Mangrove			
Water depth (m)	†0.63 (0.06)	0.88 (0.03)	1.33 (0.13)
Prop-root density (m^{-3})	25.6 (10.1)	35.8 (13.8)	70.5 (18.8)
Prop-root length (m)	†0.34 (0.03)	0.59 (0.04)	0.85 (0.10)
Relative prop-root length (%)	62.07 (4.08)	64.07 (4.76)	76.46 (9.29)
Seagrass			
Water depth (m)	1.40 (0.10)	†3.25 (0.18)	1.21 (0.08)
Seagrass cover (%)	60.47 (6.66)	45.93 (6.90)	55.60 (8.56)
Seagrass height (m)	0.27 (0.03)	0.25 (0.01)	0.25 (0.03)
Seagrass leaf density (m^{-3})	1200 (219)	561 (102)	1403 (328)

The light trap larval counts in both habitats and the larval density collected by plankton net within the seagrass beds also show significant variation with Region (Figure 4.6). No significant correlation is apparent between the larval counts and any of the structural parameters measured (Pearson correlation: $r \leq 0.630$, $p \geq 0.05$). However, variation in larval density may be explained by variation in the habitat structure.

From the light trap counts, the mean mangrove larval population of Region 1 is significantly greater than that of Region 2 or 3 (ANOVA: $F = 3.39$, $p = 0.035$), and the mean seagrass larval supply of Region 3 is significantly higher than that of Region 1 or 2 (ANOVA: $F = 4.37$, $p = 0.014$). Comparison of the nocturnal larval population and supply within each Region shows that in Region 1 the mean mangrove count is significantly higher than the larval supply, while in Region 3 the mean seagrass count is significantly higher than larval population (Two sample T-tests: $T = 2.96$, $p = 0.003$; $T = -2.28$, $p = 0.025$ respectively). A possible explanation for this is that the mangroves of Region 1 have a better retention ability than those of the other Regions, with particularly low retention ability in Region 3. In turn this could be a reflection of the habitat structure of each Region, or circulation



(a)



(b)

Figure 4.5. Two-dimensional PCA ordination of the habitat structure parameters (normalised), for 9 Stations within (a) the mangrove and (b) the seagrass habitats. The Stations of Region 1 are represented by letters A, B, C, of Region 2 by letters D, E, F and of Region 3 by letters G, H, I. Dashed lines represent grouping of Stations at a Euclidean distance of 2, from group-average cluster analysis of a Euclidean distance matrix between the 9 Stations. Stations are clearly grouped into Regions 1, 2 and 3 in the mangrove habitat, whereas in the seagrass habitat the grouped Stations of Regions 1 and 3 overlap, with only the Stations of Region 2 clearly grouped.

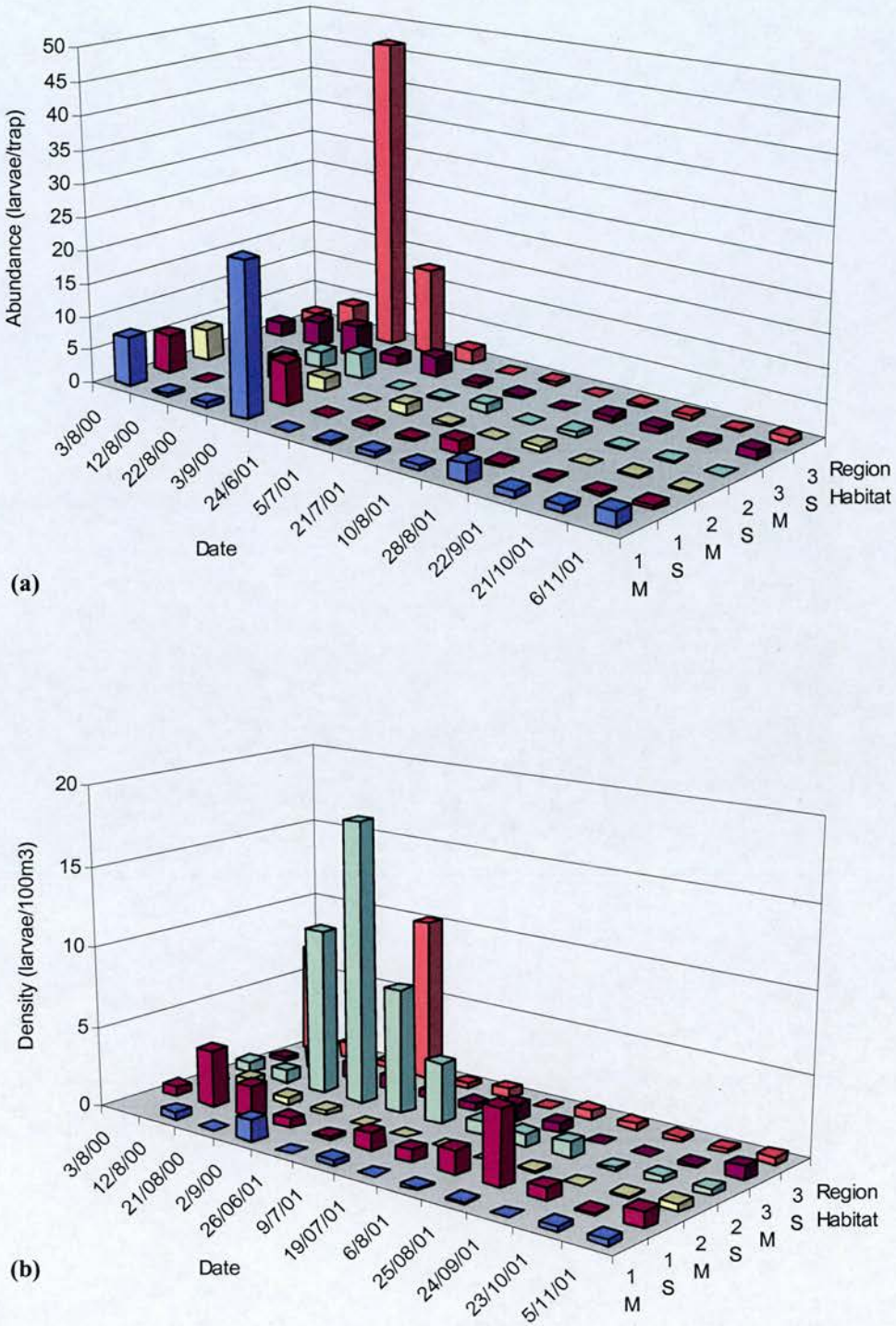


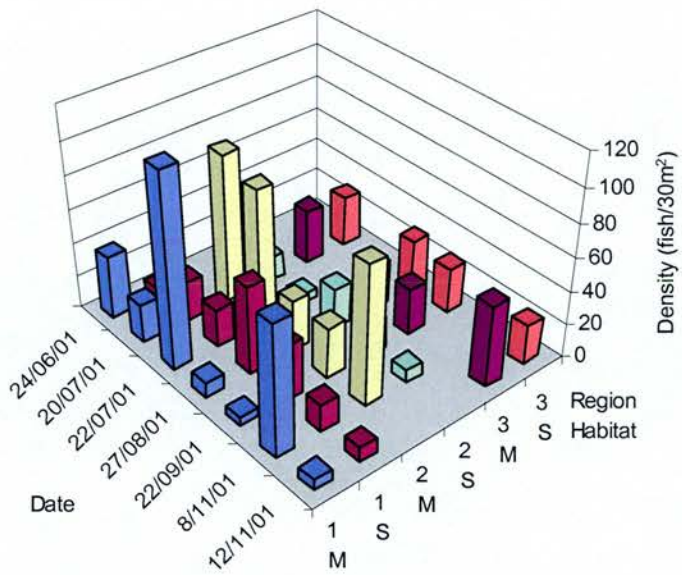
Figure 4.6. Mean abundance of larvae collected on each sampling date, in the mangrove (M) and seagrass (S) habitat of Regions 1-3, by light trap at night (a) and by plankton net during the day (b). A strong inter-annual variation is evident in all three Regions, in particular the mangroves of Region 1 and the seagrass of Region 3.

patterns, with larvae circulating from Region 3 to Region 1. Unfortunately, circulation patterns remain unstudied to date. Region 1 has the lowest mangrove prop-root density and highest percentage seagrass cover, whereas the highest density of mangrove prop-roots is in Region 3, with the intermediate percentage of seagrass cover and highest seagrass leaf density. Assuming habitat structure is an influential factor, this suggests that at night larvae prefer a relatively low prop-root density within the mangroves, and a relatively high leaf density within the seagrass.

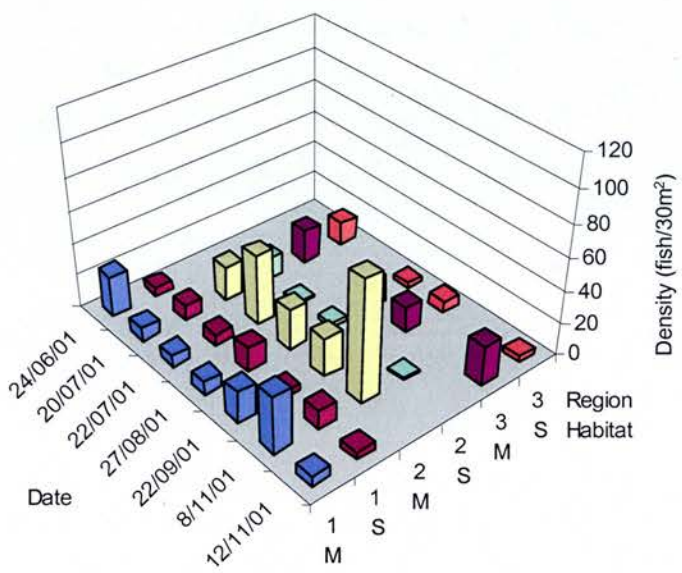
The seagrass larval supply collected by plankton net during daylight contrasts with the night observations. The mean density in the seagrass of Region 2 is significantly higher than that of Regions 1 and 3, whereas the lowest mean mangrove larval density is in Region 2. (ANOVA: $F = 0.725$, $p \leq 0.001$). Region 2 has the lowest mean seagrass leaf density as well as the lowest percentage seagrass cover. Although less shelter from predators is available to larvae as a result, there is also reduced shelter for the predators themselves during the day, leaving them more visible both to their own predators and to their prey.

Comparison of the larval population and supply within each Region shows that in Regions 1 and 2 the density of the larvae from the seagrass is significantly higher than that of the mangroves (Two sample T-test: $T = -3.32$, $p = 0.004$; $T = -3.21$, $p = 0.008$ respectively). Again, this contrasts with the observations in Region 1 at night, and indicates a diel movement of the larval assemblage between habitats.

Juvenile counts from the seagrass beds and adult counts from the mangroves both vary significantly with Region (Figure 4.7). In the seagrass beds the mean juvenile density in Region 3 is significantly higher than that of Region 2 (ANOVA: $F = 3.24$, $p = 0.048$ respectively). This contrasts directly with the larval distribution during



(a)



(b)

Figure 4.7. Mean juvenile (a) and adult (b) density per 30 m transect, recorded by visual census from the mangrove (M) and seagrass (S) habitat of Regions 1-3. For both stages, the densities collected from the mangrove habitat are significantly higher than those from the seagrass ($p < 0.05$). The seagrass juvenile density also varies significantly with Region, as does the adult density in the mangroves.

the day, suggesting that larval density is influenced by juvenile (predator) density, as well as or in addition to habitat structure. Region 3 has the highest seagrass leaf density and lowest water depth, giving limited accessibility to adults, potential predators of juveniles. Region 2 offers greater accessibility, with the lowest leaf density and greatest water depth.

In the mangroves the mean adult fish count of Region 2 is significantly higher than that of Region 1 (ANOVA: $F = 3.85$, $p = 0.029$). The structural parameters of Region 2 are intermediate between the lowest values in Region 1 and the highest values in Region 3. The low root density and water depth of Region 1 provides little shelter for adults, or for their prey, whereas the high prop-root density of Region 3 limits access to adults while providing extensive shelter to potential prey.

Neither juveniles nor adults show a significant difference in density between Stations nested within Regions (Hierarchical ANOVA: $F = 1.76$, $p = 0.132$; $F = 1.27$, $p = 0.291$ respectively). As with the night larval assemblage, this indicates that habitat parameters influence densities on the relatively large spatial scale of Regions situated approximately 1 km apart, but not at the smaller spatial scale of Stations approximately 100 m apart. However, the only factor to show a statistically significant correlation with any assemblage density is the percentage seagrass cover, with the seagrass adult density (Pearson correlation: $r = 0.685$, $p = 0.042$). While increasing seagrass cover provides more shelter for adults, it also provides more food for herbivorous species, and more shelter for potential prey.

In discussing the amount of shelter provided by both habitats, there is an underlying assumption that general fish size increases with each life stage, with juveniles and adults being small and large in size, respectively. As the two stages overlap considerably in terms of body

size due to different species, the influence of abiotic variables on fish distribution may be a reflection of body size, as well as life stage.

Habitat parameters and fish size

In the combined mangrove larval assemblage, only the 0.5 – 1.0 cm size class shows significant spatial variation, with a higher density in Region 1 than in the more structurally complex Region 3 (ANOVA: $F = 3.63$; $p = 0.030$). The larger sizes of 1.5 – 2.0 and 3.5 – 4.0 cm show a positive correlation with prop-root length and relative root length respectively (Pearson correlation: $r = 0.693$, $p = 0.038$; $r = 0.905$, $p \leq 0.001$). The water depth, root length and density all correlate strongly with the density of the 2.0 – 2.5 cm size class. This suggests that for smaller larvae the lack of shelter for predators is probably important, whereas for larger larvae the amount of shelter from predators is important.

The juvenile size class of 20 – 25 cm in the mangrove assemblage has a significantly higher abundance in Region 2 than the less structurally complex Region 1 (ANOVA: $F = 3.58$, $p = 0.036$). The larger size class of 30 – 35 cm correlates with the root density, but no other correlation is apparent. The adult size class of 5 – 10 cm follows the overall adult pattern, with a significantly higher density in the mangroves of Region 2 than Regions 1 or 3 (ANOVA: $F = 3.58$, $p = 0.036$). No significant correlation is evident between any of the size classes and the mangrove structural parameters. Region 2 offers more protection from predators, but also more shelter and therefore camouflage for predators themselves.

In the seagrass, the larval density of the 0.5 – 1.0 cm size class in Region 1 is significantly higher than in Regions 2 and 3, reflecting the mangrove larvae (ANOVA: $F = 4.58$, $p = 0.012$). The 1.5 – 2.0 cm size class has a significantly higher density in Region 3 than Region 2 (ANOVA: $F = 3.84$, $p = 0.024$), and shows a positive correlation with

seagrass leaf density (Pearson correlation: $r = 0.998$, $p = 0.040$). As the structure of the seagrass habitat in Regions 1 and 3 is more complex than in Region 2, more shelter is available for small larvae in the relatively high seagrass cover and density.

None of the juvenile size classes show a significant spatial variation in density in the seagrass, although the 35 – 40 cm size class does show a positive correlation with water depth (Pearson correlation: $r = 0.997$, $p = 0.049$). Two of the adult size classes vary significantly with Region, however. The density of 5 – 10 cm adults is significantly greater in Region 2 than 3, reflecting the mangrove density (ANOVA: $F = 3.87$, $p = 0.029$). The density of 15 – 20 cm adults is significantly higher in Region 3 than in Regions 1 or 2 (ANOVA: $F = 3.37$, $p = 0.044$). The low structural complexity of Region 2 provides little shelter for the small adults, which may compensate by gathering in high densities. For the larger adults, the high structural complexity of Region 3 provides an extensive food source both in terms of seagrass and algae for herbivores, and prey organisms that inhabit the seagrass. Similarly, larger adults 25 – 30 cm in size show a positive correlation with seagrass cover and height, while adults 95 – 100 cm in length also correlate with seagrass leaf height (Pearson correlation: $r \geq 0.670$, $p \leq 0.048$).

Environmental variables and fish densities

As the densities of the daytime larval, juvenile and adult assemblages vary significantly between the mangrove and seagrass habitats, so do the environmental variables measured in addition to the habitat parameters (2-way crossed ANOSIM: $R = 0.167$, $p \leq 0.001$). These environmental variables exhibit little spatial variation within each habitat on a Regional scale, although both the salinity and nitrate ion concentration of the seagrass beds vary significantly with Region (Table 4.3). Neither they nor the remaining variables show significant correlation with fish density of any life stage, however. A clear trend

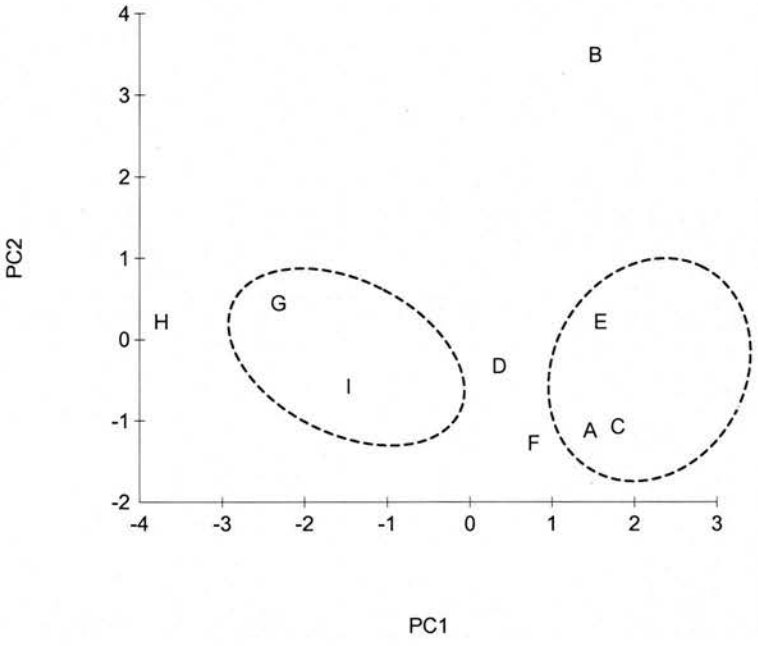
of changing levels of environmental variable with Station is evident for both habitats (Figure 4.8).

Table 4.3. Mean values ± standard error of environmental variables measured in the mangrove and seagrass habitats of Regions 1, 2 and 3. The symbol † indicates a significantly different mean ($p < 0.05$) when present singly, or 2 significantly different means when present in a pair.

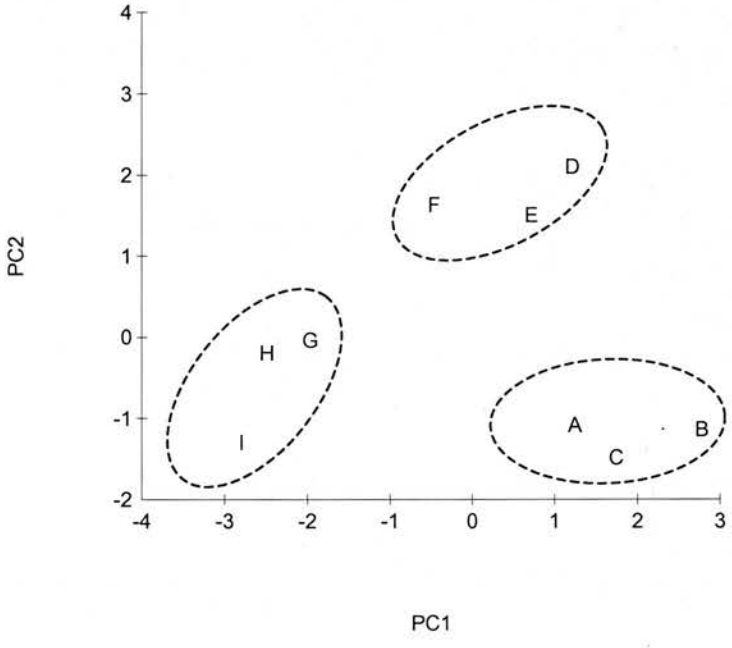
	Regions		
	1	2	3
Environmental variables			
Mangrove			
Water temperature (°C)	29.51 (0.22)	29.43 (0.21)	28.89 (0.33)
Extinction coefficient	1.49 (0.25)	1.23 (0.18)	1.23 (0.20)
Wind velocity (m/s)	2.50 (0.40)	2.51 (0.45)	†1.00 (0.20)
Turbidity (FTU)	0.94 (0.68)	0.56 (0.27)	0.78 (0.34)
Sulphate (mg/l)	180.5 (1.9)	179.1 (2.2)	175.8 (2.5)
Nitrate (mg/l)	0.11 (0.02)	0.10 (0.01)	0.13 (0.02)
Salinity (‰)	36.73 (0.13)	36.64 (0.12)	36.54 (0.25)
pH	8.14 (0.11)	8.17 (0.02)	8.15 (0.03)
Seagrass			
Water temperature (°C)	29.28 (0.20)	29.26 (0.20)	28.64 (0.25)
Extinction coefficient	0.94 (0.06)	0.95 (0.10)	0.73 (0.05)
Wind velocity (m/s)	3.00 (0.39)	3.28 (0.49)	2.53 (0.35)
Turbidity (FTU)	0.56 (0.32)	0.42 (0.23)	0.28 (0.19)
Sulphate (mg/l)	175.2 (2.0)	177.4 (2.0)	173.6 (2.0)
Nitrate (mg/l)	†0.21 (0.04)	†0.12 (0.02)	0.14 (0.02)
Salinity (‰)	†37.56 (0.22)	36.90 (0.14)	36.89 (0.19)
pH	8.27 (0.03)	8.22 (0.02)	8.19 (0.02)

In both habitats the combined environmental variables matrix differs significantly on the scale of Stations nested within Regions, but not at the Regional scale (Nested ANOSIM: $R \geq 0.473$, $p \leq 0.032$; $R \geq -0.056$, $p = 1.00$ respectively). This contrasts with the habitat parameters, indicating that environmental variables are likely to influence variation on the scale of Stations rather than Regions.

Although the mean densities of the night larval population and supply both show a significant difference between Regions, neither varies significantly between Stations nested within Regions (Hierarchical ANOVAS: $F = 0.380$, $p = 0.892$; $F = 1.58$, $p = 0.155$ respectively). Similarly, no significant difference in mean juvenile or adult fish density is evident between Stations nested within Regions in either the



(a)



(b)

Figure 4.8. Two-dimensional PCA ordination of the environmental variables (transformed and normalised), for 9 Stations within the mangrove (a) and the seagrass (b) habitats. The Stations of Region 1 are represented by letters A, B, C, of Region 2 by letters D, E, F and of Region 3 by letters G, H, I. Dashed lines represent grouping of Stations at a Euclidean distance of 2, from group-average cluster analysis of a Euclidean distance matrix between the 9 Stations. Grouping of Stations into Regions 1, 2 and 3 is very clear in the seagrass habitat, whereas in the mangrove habitat only the Stations of Region 3 are clearly grouped.

mangrove or seagrass habitats (Hierarchical ANOVA; $F \leq 1.76$, $p \geq 0.132$). This suggests that on a spatial scale the combined matrix of the measured environmental variables does not influence the overall density of any of the life stages.

Environmental variables and fish size

The individual size classes of each life stage do show some variation on the scale of Stations, however. In the seagrass beds, larvae of 0.5 – 2.0 cm vary significantly in abundance between Stations nested within Regions (ANOVA: $F \geq 2.26$, $p \leq 0.041$). No correlation is evident between larval counts and environmental variables in the seagrass, however. Correlation is evident in the mangrove habitat, between the density of < 0.5 cm larvae and the extinction coefficient, 0.5 – 1.0 larvae and temperature, and 2.0 – 2.5 larvae and nitrate ion concentration (Pearson correlation: $r \geq 0.670$, $p \leq 0.048$).

No variation by Station is evident in the juvenile densities of either habitat. However, the density of 25 – 30 cm juveniles is positively correlated with both sulphate ion concentration and wind speed in the mangroves (Pearson correlation: $r = 0.808$, $p = 0.008$; $r = 0.736$, $p = 0.023$ respectively). Adults show no correlation with individual environmental variables in the mangroves, but the density of the 15 – 20 cm size class varies significantly with Stations nested within Regions (ANOVA: $F = 3.23$, $p = 0.012$). In the seagrass 20 – 25 cm adults vary significantly between Stations (ANOVA: $F = 2.64$, $p = 0.032$). Significant correlation with environmental variables is only evident in adults < 5 cm in length, which correlate with the salinity and water temperature of the seagrass beds (Pearson correlation: $r = 0.669$, $p = 0.049$; $r = 0.686$, $p = 0.411$ respectively). The range in the levels of environmental variables is relatively small, and likely to have more effect on the smaller and younger life stages.

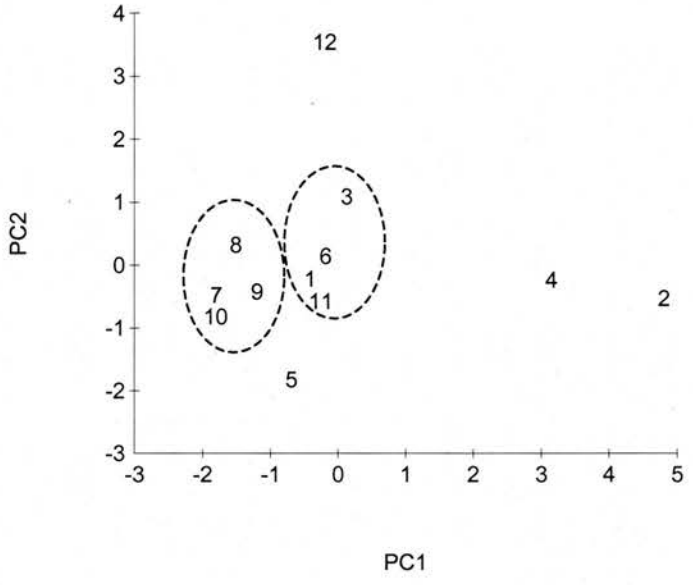
Key points

Overall, it seems that environmental variables as well as habitat structure influence the spatial distribution of the three main life stages of reef fish, especially in the different size classes. The key points apparent in the spatial variation of abiotic variables and fish assemblages within each habitat are summarised as:

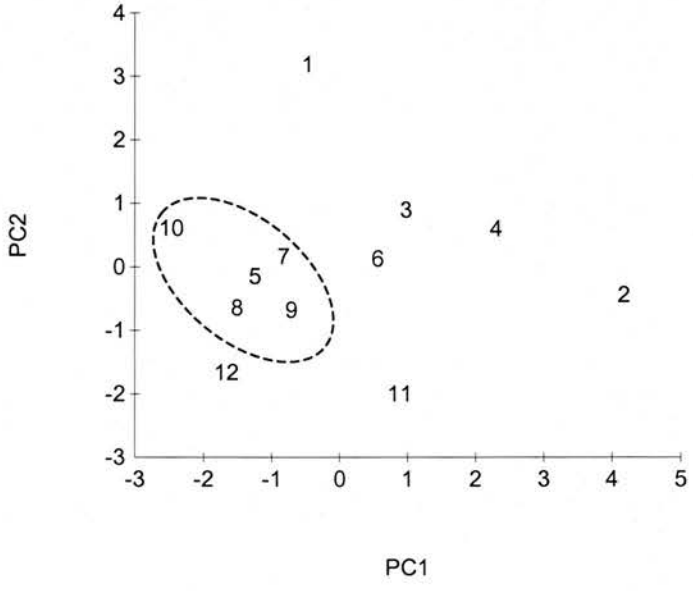
- In both the mangroves and seagrass, habitat structural parameters vary significantly with Region;
- variation with Region, and by association habitat structure, is apparent in the overall density of larvae at night in both habitats, larvae and juveniles in the seagrass during the day, and adults in the mangroves;
- diel movement between habitats is apparent for the larval assemblage in Region 1, with higher densities in the seagrass during the day and in the mangroves at night;
- environmental variables vary significantly with Stations nested within Regions in both the mangroves and seagrass;
- no variation with Stations nested within Regions is evident for the overall larval, juvenile or adult assemblage densities in either habitat;
- the spatial distribution of individual size classes of larval, juvenile and adult fish is correlated with individual environmental factors.

4.2.3. Comparison of temporal variation of environmental variables and larval assemblage density

The environmental variables measured all vary with time (Appendix 4.1), and are therefore a potential influence on the temporal variation of the larval assemblages. A clear trend of changing levels of the environmental variables with sampling date is evident in both the mangrove and seagrass habitats (Figure 4.9). Significant inter- and intra-annual variation is apparent in the combined environmental variables matrix (2-way crossed ANOSIM: $R = 0.493$, $p \leq 0.001$).



(a)



(b)

Figure 4.9. Two-dimensional PCA ordinations of the plankton net sampling dates, based on 8 environmental variables (wind speed, extinction coefficient, water temperature, pH, sulphate ion concentration, nitrate ion concentration, salinity and turbidity) for the mangrove (a) and seagrass (b) habitats. For visual clarity sampling dates have been labelled consecutively with 1 – 12 representing 03/08/2000 – 05/11/2001 respectively. A clear trend of changing levels of the environmental variables with sampling date is evident in both habitats. Dashed lines represent grouping of Stations at a Euclidean distance of 3, from group-average cluster analysis of a Euclidean distance matrix between the 12 dates.

Each individual variable also shows significant temporal variation, both inter- and intra-annually (ANOVA: $F \geq 2.86$, $p \leq 0.003$). During the day, both the larval population and supply show significant inter-annual variation, with higher mean densities in 2000 than 2001, and no significant intra-annual variation (ANOVA: $F = 2.18$, $p = 0.022$; $F = 2.04$, $p = 0.033$ respectively). At night a significant inter-annual variation in larval density is also evident in both habitats, with higher values in 2000 than 2001 (ANOVA: $F = 4.92$, $p \leq 0.001$; $F = 12.75$, $p \leq 0.001$ respectively). Again, no significant difference is evident in the overall larval abundance between the months within each year.

Although intra-annual variation is not statistically significant, it is apparent in 2000 during which sampling was conducted on 4 occasions over a full tidal and lunar cycle. The highest larval counts in 2000 occur on the 1st, 3rd and 4th sampling dates, which in turn correspond with the 1st, 3rd and last quarters of the lunar cycle, while the lowest mean counts of both larval population and supply occur during the 2nd quarter of the lunar cycle, running up to the full moon.

Temporal variation in density is not evident across all the larval size classes. In the mangroves, < 0.5 and 1.0 – 1.5 cm larvae show significant inter- and intra-annual variation in abundance (ANOVA: $F = 2.29$, $p = 0.003$; $F = 2.96$, $p \leq 0.001$ respectively). In the seagrass, inter- and intra-annual variation is evident in larvae ≤ 2.5 cm, and 4.5 – 5.0 cm.

Despite the temporal variation evident in the larval densities of both habitats during the day and night, only the density of larvae collected during the day in the mangroves, and turbidity show significant correlation (Pearson correlation: $r = 0.751$, $p = 0.005$). However, when broken down into individual size classes, correlation is also evident between the extinction coefficient and 0.5 – 1.0 cm larvae (Pearson

correlation: $r = 0.641$, $p = 0.024$). Turbidity is correlated with 1.0 – 1.5 cm larvae, as is the extinction coefficient and sulphate ion concentration (Pearson correlation: $r \geq 0.614$, $p \leq 0.004$). In the seagrass habitat turbidity correlates with the abundance of 1.5 – 2.0 and 3.5 – 4.5 cm larvae (Pearson correlation: $r \geq 0.611$, $p \leq 0.001$).

Overall, it appears that the smaller larval size classes in the mangroves and the larger larvae in the seagrass benefit from increasing turbidity, and decreasing light intensity in the former habitat, both of which make them less visible to predators.

Key points

The temporal variation of environmental variables and larval assemblage density may be summarised as:

- the environmental variables show significant inter- and intra-annual variation;
- the day and night larval assemblages of both habitats show significant inter-annual variation in total density;
- inter- and intra-annual variation is evident in the mangrove < 0.5 and 1.0 – 1.5 cm size classes, and all 0.5 cm size classes < 2.5 cm, and 4.5 – 5.0 cm in the seagrass.
- the temporal variation of smaller larvae (< 1.5 cm) is correlated with the extinction coefficient, sulphate ion concentration and turbidity in the mangroves;
- the temporal variation of larger larvae (> 1.5 cm) is correlated with turbidity in the seagrass habitat.

4.3. *Discussion*

Reef fish may be expected to select habitats which maximise survival by offering the most shelter and food, and consequently display a preference for more complex habitats. While the active selection of habitats is hard to detect and define without direct experimentation, the settlement patterns of fish within the mangrove or seagrass habitats

may be indicative of a preference for either habitat type. Settlement by definition occurs prior to, during or after fish metamorphosis, from the larval to juvenile stage (Caley *et* al., 1996; Fraschetti *et al.*, 2003). Although larval distribution provides an indication of potential settlement patterns, the point at which active habitat selection occurs is hard to define (Dennis, 1992; Thorrold *et al.*, 1994; Cowen & Sponaugle, 1997). The larval assemblage composition of the present study therefore indicates the taxa available to settle, which, when compared with distribution patterns of subsequent life history stages, in turn indicates whether larval supply is a significant determinant of juvenile and adult distribution.

In answer to the initial research question of whether the different life stages of reef fish prefer one habitat over another, it initially appears from absolute abundances that larvae prefer seagrass while juveniles and adults prefer mangroves. The dominance of the smallest size classes (< 1.5 cm) in the larval assemblages of both habitats indicates a high supply of young larvae. The close proximity of Calabash to the outer reef, and the presence of channels in the reef crest, in turn suggests a large proportion of the larval supply consists of pelagic larvae. Despite a high larval supply, larval retention in the mangroves appears to be low, implying that settlement is higher in the seagrass. The smallest size class of < 0.5 cm consists of larvae only a few days old, and has a significantly higher density in the seagrass than in the mangroves.

Seagrass leaves offer a finer habitat structure than mangrove prop roots, and better shelter for smaller organisms (Ogden & Ehrlich, 1977; Shulman, 1984; Rooker & Dennis, 1991). Overall, the mean larval body size in the mangroves exceeds that in the seagrass, indicating that the mangroves are the preferred habitat of the larger and, therefore possibly older, individuals. Such individuals may have outgrown the

shelter available in the seagrass beds, but are also less susceptible to predation due to their larger size.

Significantly lower juvenile reef fish densities are evident in the seagrass than in the mangrove prop roots, and again may be explained by juveniles outgrowing the shelter available in the seagrass and being less susceptible to predation. This is supported by the mean juvenile body size, which is significantly greater in the mangroves than in the seagrass. The density of the smallest size class (< 5 cm) does not differ significantly between the two habitats, while the next three classes (5 – 20 cm) are significantly more abundant in the mangroves. The mangroves also seem preferable to larger, and therefore older, adults. The two smallest adult size classes (< 10 cm) do not differ significantly in density between the two habitats, but 10 – 30 cm adults have a significantly higher abundance in the mangroves.

The marked decrease in species richness from 120 larval taxa to 50 juvenile taxa indicates loss through migration between habitats, cryptic behaviour, and natural mortality. Larvae are able to control their direction of travel by vertical orientation in the water column, maximising the effect of tidal currents or wind-induced surface currents, and some species are competent swimmers, capable of actively modifying their dispersal patterns (Heath, 1992; Cowen & Sponaugle, 1997; Stobutzki & Bellwood, 1997; Leis & Carson-Ewart, 1999; Fisher & Bellwood, 2000, 2002; Fisher *et al.*, 2000). Thus fish have the ability to actively migrate from the mangrove and seagrass habitats of Calabash at both the larval and juvenile stages, either to the outer coral reef environment or into more sheltered areas of the lagoon. Despite the early swimming ability apparent for some fish, larvae are also removed from inshore populations by offshore transport processes, such as tidal currents or wind-induced surface currents (Heath, 1992). A further level of "loss" of taxa is due to the development of cryptic behaviour following metamorphosis. Many of the taxa collected here

as larvae are likely to be poorly represented in visual census surveys due to cryptic behaviour as juveniles and adults. These include members of the suborder Blennioidei and the family Gobiidae, two of the more abundant groups of larvae collected.

Natural mortality mainly takes the form of predation, starvation or disease. In the highly productive mangrove and seagrass ecosystems, starvation and disease are unlikely to be major sources of mortality, whereas the restricted amount of habitat and high density of fauna makes predation a more likely factor. However, the knowledge of larval interaction with predators is limited (Carr & Hixon, 1995; Leis & Carson-Ewart, 1999).

The physical and chemical characteristics of shallow water habitats are associated with fish distribution on a behavioural scale (Kramer *et al.*, 1997), but their effect is difficult to separate from biotic factors such as predation and food availability. The second research question posed is whether other abiotic variables in addition to habitat type influence the density and size distribution of each life stage. The environmental variable matrix shows a significant small-scale variation at scales of 100s of metres, but not at scales of 1000s of metres, while the opposite is apparent for the structural parameters of both habitats. Variation with Region, at scales of 1000s of metres and therefore with habitat structure, is apparent in the overall density of larvae at night in both habitats, larvae and juveniles in the seagrass during the day, and adults in the mangroves.

A diel variation in spatial distribution of larvae is apparent, with movement from the mangroves to the seagrass at night and vice versa during the day. This could be an effect of changes in stratification, which is much reduced in larval assemblages at night (Rooker *et al.*, 1996). Nevertheless, the nocturnal spatial distribution of larvae favours a relatively low prop-root density in the mangroves and a

relatively high leaf density in the seagrass habitats, while the diurnal larval densities are greatest in seagrass areas of low leaf density and cover. Distributions are likely to be reflecting predator movements, many of which leave the shelter of the mangroves to feed in seagrass beds at night. Predation pressure on larvae would therefore be less in mangroves at night, but higher in the seagrass, prompting a preference for the increased shelter provided by dense seagrass. Similarly, diurnal predator presence in low density seagrass is likely to be low due to the limited amount of shelter available. Preference for low seagrass density indicates that the risk of photodamage is low, implying in turn that the use of sheltering factors such as turbidity or extinction coefficient is a reaction to predation pressure. Within the seagrass habitat during the day, juveniles and adults show a preference for relatively high leaf density and cover, and for mangroves where the adjoining seagrass habitat has a low mean leaf density and cover. High seagrass cover provides shelter not only for adults, but also for potential prey organisms, thereby providing an extensive food source for carnivorous as well as herbivorous species.

Adult densities are greatest in areas in which the structural parameters of the mangrove habitat are intermediate. A low root density and low water depth provides little shelter and limits the water column available for adults or their prey (Valdés-Muñoz & Mochek, 2001), whereas a high prop-root density limits access to adults while providing extensive shelter to potential prey organisms. The influence of individual structural parameters of the mangrove and seagrass habitats varies according to the body size of the various reef fish life stages.

Within the mangroves, the densities of all larvae < 4.0 cm are influenced by habitat factors. Significant spatial variation in small (0.5 – 1.0 cm) larvae may be due to the arrival of larval pulses through channels in the reef, prior to any circulation around Calabash taking effect. Larger juveniles (30 – 35 cm) are influenced by the mangrove

prop-root density, probably in terms of shelter availability. None of the adult size classes appear to be influenced by individual habitat factors, implying each is of the same importance to all sizes. Larger juveniles (20 – 25 cm) and small adults (5 – 10 cm) both show a preference for mangroves of intermediate structural complexity. Both are susceptible to predators, and a low root density and water depth provides little shelter, whereas a high prop-root density limits access to potential prey organisms and shelter.

In the seagrass, the distribution of small larvae (0.5 – 2.0 cm) is influenced by shelter availability, in terms of seagrass leaf density and percentage cover. Juvenile size classes are not strongly influenced by habitat structure, although larger fish (35 – 40 cm) show a preference for increased water depth. Small adults are abundant in areas with low structural complexity, which may provide good access to prey organisms, and also enables dense schooling, a defensive tactic. Larger adults show a preference for seagrass of a high structural complexity, which may provide an extensive food source for both herbivores and carnivores, as well as shelter.

The spatial distribution of individual size classes of larval, juvenile and adult assemblage densities also show some linkage to the environmental variables. In the seagrass beds, younger larvae (0.5 – 2.0 cm) and the environmental variable matrix show small scale variation between Stations, which may be a reflection of circulation patterns. In the mangroves, larvae < 0.5 cm are correlated with the extinction coefficient, thereby decreasing the risk from both photodamage and predation. Larvae 0.5 – 1.0 cm in length are correlated with temperature, and 2.0 – 2.5 larvae with nitrate ion concentration, both of which could be reflections of circulation patterns: both variables are likely to be higher in more sheltered regions with lower water circulation, which may also be retaining larvae.

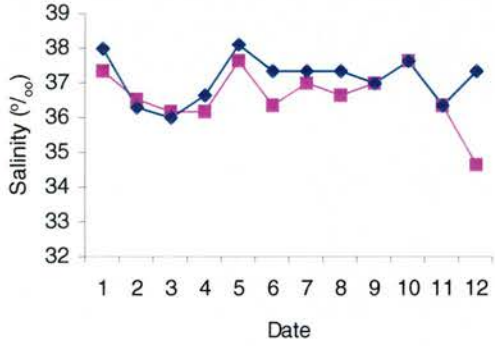
Juveniles of 25 – 30 cm are correlated with sulphate ion concentration and wind velocity in the mangroves, which are probably related in turn: onshore wind-driven water currents will lower flushing of the mangrove habitat, resulting in higher ionic concentrations. In the mangroves and seagrass respectively, adults of 15 – 20 cm and 20 – 25 cm and the environmental variable matrix show small scale variation between Stations, which may be a reflection of circulation patterns. Small adults (< 5 cm) in the seagrass beds show correlation with salinity and water temperature, both of which are again indicators of circulation and flushing.

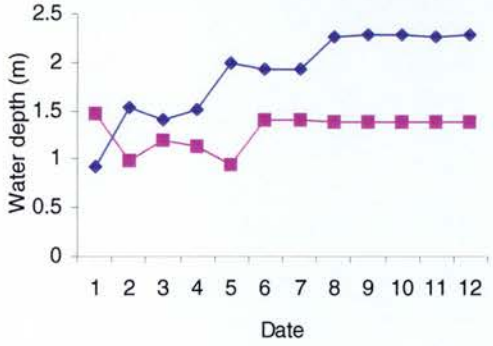
With regard to the final research question, the environmental factors show significant inter- and intra-annual variation, both as a combined matrix and individually. Significant inter- and intra-annual variation is also evident in the abundance of small larvae in the mangroves, and larger larvae in the seagrass, with higher densities in 2000 than 2001. A wide size range of larvae is correlated with turbidity in both the mangroves and the seagrass, and with the extinction coefficient in the mangroves. Both factors offer increased protection from the risks of photodamage and predation (Morgan & Christy, 1996).

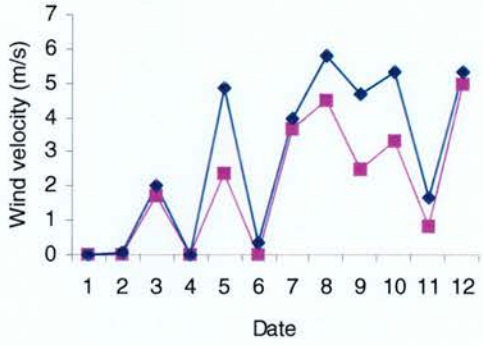
The night and day larval assemblages show a stronger correlation with the environmental variables in the seagrass than the mangrove habitat. Although no single abiotic factor appears to be a major influence, several vary significantly between habitats. Of these, the mean extinction coefficient is significantly greater in the mangroves than in the seagrass, indicating that the risk of photodamage and visual predation is reduced in the mangrove prop roots. As the extinction coefficient is also correlated with many of the larval size-classes, it appears to be an influential abiotic factor, whereas the other variables that vary significantly between habitats (wind velocity, water depth, nitrate ion concentration and salinity) do not correlate significantly with larval densities. The increased extinction coefficient is likely to

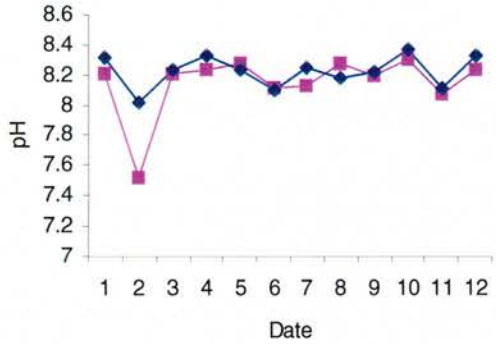
be a result of both increased turbidity in the mangroves and shade from the overhanging canopy of the mangrove trees. This is interesting with regard to the concept that more dense habitats provide more protection (Macia *et al.*, 2003), as the extinction coefficient would be expected to increase as the density of a mangrove stand, and therefore its canopy, increased. The protection provided by a habitat is generally discussed in terms of physical shelter rather than poor visual conditions (Robertson & Duke, 1987; Thayer *et al.*, 1987; Mitsch & Gosselink, 1993; Whitfield, 1999), although the concept that the indirect effects of habitat complexity may significant is not a new one (Helfman, 1981).

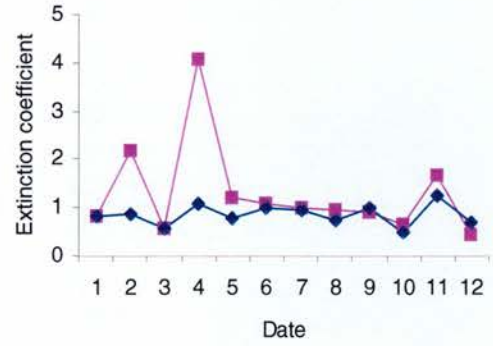
The larval abundance in the seagrass and mangrove habitats will also be influenced by factors such as the size and frequency of larval pulses, and tidal or lunar periodicity. Some indication of their degree of influence may be deduced from the temporal scale of larval supply to Calabash Cay, discussed in Chapter 5.

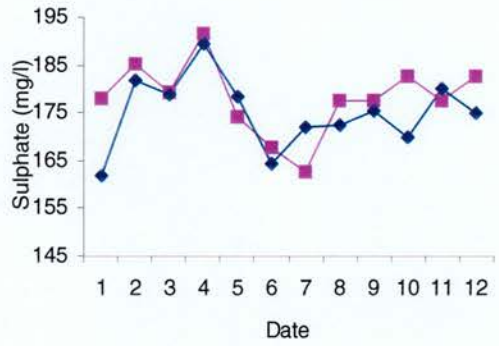


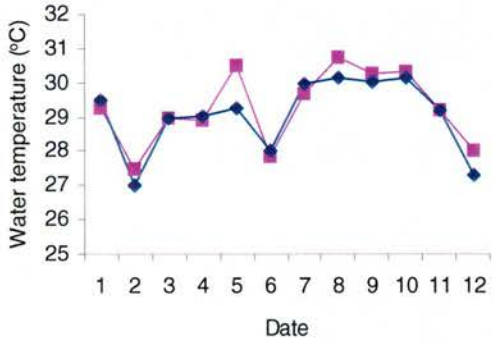


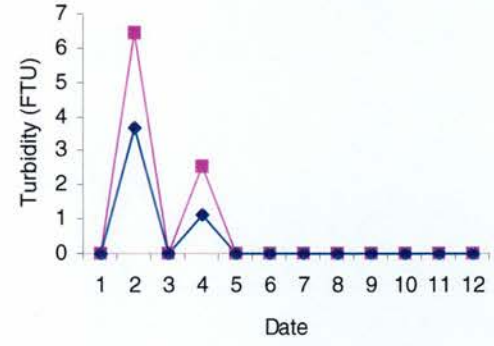


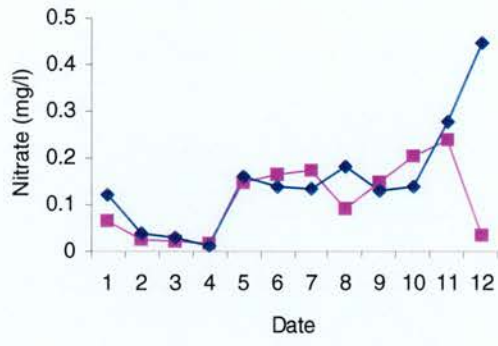












Appendix 4.1. Variation of environmental variables with time. Sampling dates are numbered 1-12 for clarity. Note that not all axes commence at 0. In the key M represents the mangroves and S the seagrass habitat.

5.0 Temporal scale of larval supply to a Caribbean coral reef lagoon

5.1 *Introduction*

Geographic variation in larval distributions produces inherent variability in the results of studies using similar methods. There is also inherent temporal variability, as demonstrated by comparison of 3 studies conducted in different years at the same site off Lizard Island, Australia, in which the mean number of fish larvae captured per light trap ranged from 1.5 to 4.9 to 190 individuals per hour respectively (Doherty, 1987; Choat *et al.*, 1993; Fisher & Bellwood, 2002). However, it appears that no studies have been conducted for longer than two consecutive years using identical light-aggregation methodology at the same site. Within-year variability due to tidal cycles and lunar phases has been detected in Caribbean (Thorrold *et al.*, 1994; Rooker *et al.*, 1996; Sponaugle & Cowen, 1996a, 1996b) and Indo-Pacific (Doherty *et al.*, 1994; Hickford & Schiel, 1999) studies, with peaks in larval numbers generally occurring with the new and three-quarter moon.

The collection of larval samples at night partly counteracts sampling problems due to the stratification of larvae, as this appears absent or reduced at night (Choat *et al.*, 1993). Studies in which diel variation in larval distributions is evident have generally found much greater numbers present at night, although this may also be a result of reduced stratification (Thorrold *et al.*, 1994). Sampling duration has rarely been considered a source of variability, with most studies assuming that the abundance of larvae collected will be proportional to the period of light trap deployment. Rooker *et al.* (1996) found an optimal catch per unit effort (catch per minute) of 10 minutes, using a nightlight lift-net. However, the maximum sampling duration used in the study was 20 minutes, and the design of the collection apparatus was reliant on

larvae remaining at the light source. By contrast, the majority of light trap designs consist of a light source enclosed in a large container with small openings, which retain captured larvae around the light (Gregory & Powles, 1988; Choat *et al.*, 1993; Brogan, 1994; Ponton, 1994; Sponaugle & Cowen, 1996a, 1996b; Hickford & Schiel, 1999; Röpke *et al.*, 1999; Meekan *et al.*, 2000; Watson *et al.*, 2002). Meekan *et al.* (2000) suggest that small entrances into light traps may decrease their efficiency due to the probability of fish encountering the openings, but simultaneously suggest that the same factor impedes escape.

Associated with the sampling duration at night is the time of night at which collections are made. Although several studies suggest this has no significant effect on the performance of light traps, no quantitative analysis has been published to date to support such an assumption (Holmes & O'Connor, 1988; Watson *et al.*, 2002). The present study evaluates the variation in larval supply under a range of temporal scales, using a nested (hierarchical) design. Two light-traps were set for 3 consecutive 2-hour periods (referred to as the first, second and third hours) in a single night. Sample collection was repeated for 3 consecutive nights in each of three weeks, in August 2001, at Calabash Cay. A full description of the methods is given in *Chapter 2*.

The research questions addressed are:

1. Is the density and size-distribution of larval supply stable across varying timescales of hours, days and weeks?
2. Does the taxonomic composition of larval supply exhibit variation over differing temporal scales?

5.2 *Results*

5.2.1 Density and size-distribution of larval supply

The transformed counts of the two traps do not differ significantly, enabling the count data to be pooled for further analysis (Two sample

T-test: t = 0.47, p = 0.64). The highest mean larval abundance per sample was collected in the second week of sampling (Figure 5.1).

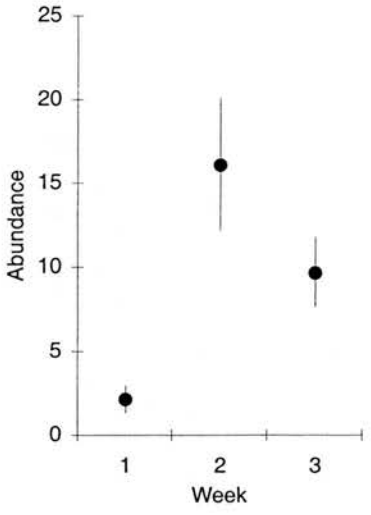


Figure 5.1. Mean larval abundance, ± standard error, per sample. Calculated for each week using pooled data from two traps. The count of week 1 is significantly lower than those of weeks 2 and 3.

Total larval counts differ significantly between successive weeks and days nested within weeks (Hierarchical ANOVA: F = 22.14, $p \leq 0.001$; F = 4.03, p = 0.005 respectively). The larval counts per hour do not vary significantly when nested within weeks and days, indicating that the time of night at which sampling was done had no significant effect (Hierarchical ANOVA: F = 1.97, p = 0.054). The greatest variance, of 17 %, is due to weeks, with the variance due to days and hours much lower at 7 % and 5 % respectively.

A Tukey's pairwise comparison of weeks shows that the mean larval abundance collected is significantly lower in week 1 than in weeks 2 and 3. No significant difference in mean larval abundance is evident between weeks 2 and 3. The full moon occurred during the first week, lessening the effectiveness of the traps and also increasing predation risk by increasing visibility. In weeks 2 and 3 incident moonlight is reduced with the three-quarter and new moon respectively. In both cases predation risk is reduced and the effectiveness of the light traps increased.

Division of the larvae into size classes of 0.5 cm increments shows a relatively high abundance of small larvae, < 1.5 cm in body length (Figure 5.2). The densities of larvae in the first three size classes differ significantly from all the remaining size classes, and from each other (ANOVA: $F = 61.54$, $p \leq 0.001$).

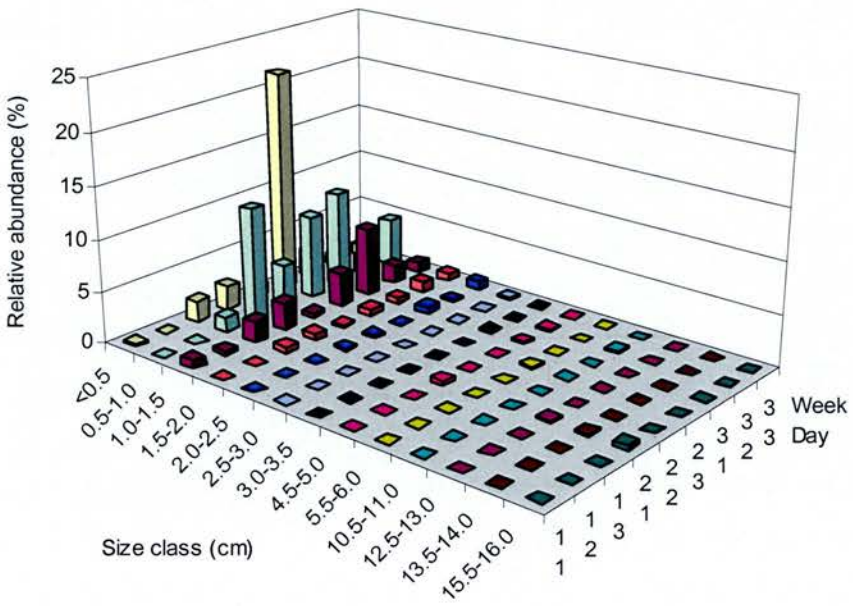


Figure 5.2. Relative abundance (%) of larvae in standard length size classes, of 0.5 cm increments. Calculated as a percentage of the entire larval assemblage. The densities of larvae in the first three size classes differ significantly from all the remaining size classes, and from each other, but only < 0.5 cm larvae show any significant temporal variation in abundance, and only with days nested within weeks ($p < 0.05$).

Only < 0.5 cm larvae show any significant temporal variation in abundance, and only with days nested within weeks (Hierarchical ANOVA: $F = 3.51$, $p = 0.003$). The size-distribution of larvae between weeks, and between hours nested within weeks and days, appears to be relatively stable.

Key points

The key points of the temporal variation of larval supply density and size-distribution may be summarised as:

- total larval density varies significantly on the scale of weeks, and days nested within weeks, but not between hours nested within days and weeks;
- week 2 has the highest mean larval abundance;
- the larval densities of weeks 2 and 3 are significantly higher than that of week 1;
- the larval assemblage in all 3 weeks is predominated by larvae < 1.5 cm in length;
- only < 0.5 cm larvae show a significant temporal variation, and only between days nested within weeks.

5.2.2 Assemblage composition

A total of 39 taxa within 23 families, were identified from the light trap samples (Appendix 5.1). A single larva remains unidentified. For initial analysis of sample composition, the Shannon diversity index (H') and Margalef's index of species richness (d) were calculated for each sample. The greatest mean values per sample of both H' and d are in week 2 (Figure 5.3).

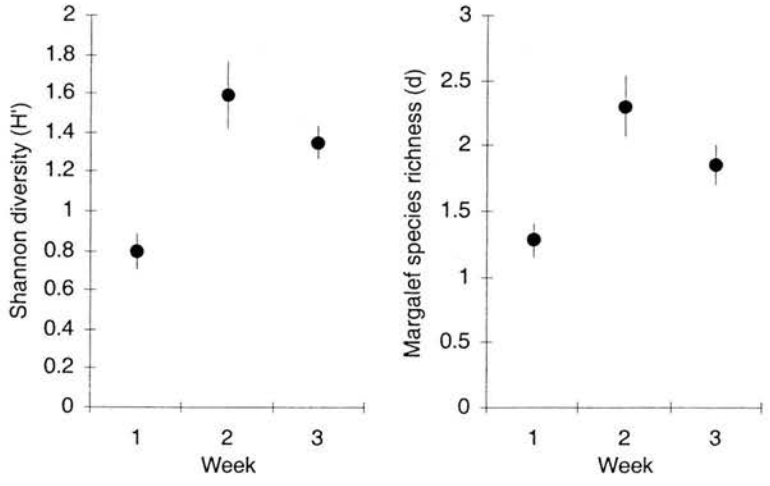


Figure 5.3. Mean Shannon diversity (H') and Margalef species richness values (d), ± standard error, calculated for each week from pooled light trap data. Week 1 has notably lower values than weeks 2 and 3.

No significant difference is evident between the median H' values of the two traps, enabling data to be pooled for further analysis (Mood's Median: $\chi^2 = 0.39$, DF = 1, p = 0.531). The median H' value of week 2 is significantly higher than that of week 1, according to a Tukey-type non-parametric multiple comparison on the pooled trap data (Kruskal-Wallis: $H = 8.66$, df = 2, p = 0.013; Dunn's test: q = 2.94, p < 0.05). Similarly, the Margalef species richness of week 2 is also significantly greater than that of week 1 (Kruskal-Wallis: $H = 7.78$, df = 2, p = 0.020; Dunn's test: q = 2.74, p < 0.05). Zero values prevent comparison of diversity of samples at the levels of days or hours.

Principal components analysis (PCA) was used to analyse both diversity indices together (Figure 5.4). The majority of variation is accounted for by the first two axes (PC1 = 85.3%, PC2 = 12.6%), illustrating the greater diversity of species in week 2 compared with weeks 3 and 1.

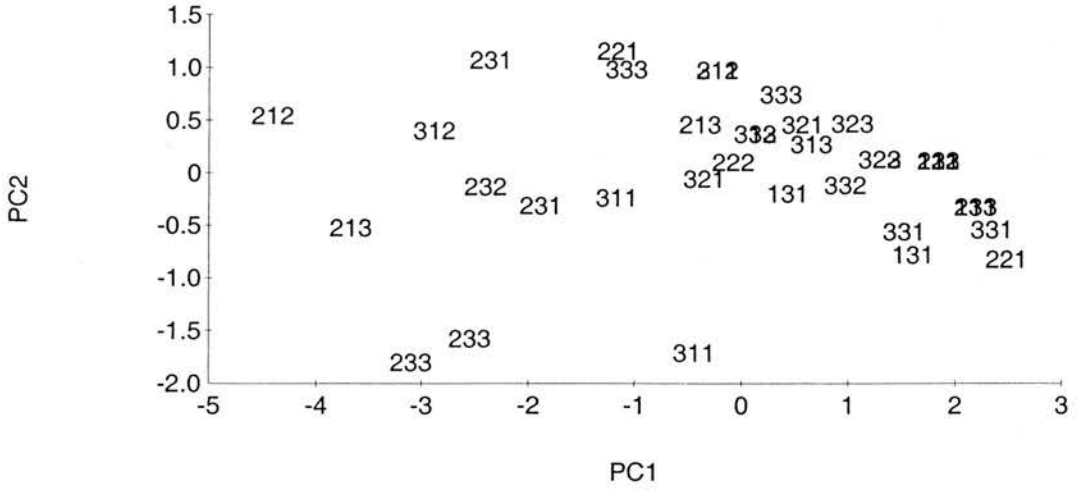


Figure 5.4. 2-dimensional PCA ordination of diversity indices (Shannon's diversity index and Margalef's index of species richness) of all samples. PC1 (x-axis) and PC2 (y-axis) account for 97.9% of total variability. Sample labels *jkl* represent week, day, hour. The majority of variation is accounted for by the first two axes (PC1 = 85.3%, PC2 = 12.6%), indicating a greater diversity of species in week 2 compared with weeks 3 and 1.

Direct comparison of the assemblage compositon of the traps shows no significant distinction due to the traps at either the species or family

level (ANOSIM: R = -0.004, p = 0.511; R = -0.04, p = 0.902 respectively), indicating that the composition of samples was not greatly affected by the individual traps or their positioning. Although a clear community pattern is not readily discernable from cluster analysis of the sample compositions, some grouping of weeks is apparent (Figure 5.5).

The distinction of weeks is confirmed by a significant variation evident between the assemblage composition of samples by week, and days nested within weeks, at both taxonomic levels (Nested ANOSIM: $R \geq 0.128$, $p \leq 0.043$). In contrast, the time of night appears to have no significant effect on the species or family composition when nested within weeks or days (Nested ANOSIM: $R \leq 0.061$, $p \geq 0.183$).

A similarity percentages (SIMPER) routine shows that approximately two thirds of the dissimilarity between week groups is accounted for by 21 taxa out of a possible total of 39 (Table 5.1). Both *Atherinomorus stipes* and *Jenkinsia parvula* are present across all the cluster groups. The abundance of *A.stipes* is low in both of the week 1 clusters, high in both of the week 2 clusters and intermediate in both of the week 3 clusters, indicating that its abundance is partly responsible for differences between the assemblages of each week.

The counts of *J.parvula* are relatively low across all the groups, indicating that its abundance is not a determining factor in the clustering of the groups. Although the clusters do show strong grouping of samples by week, there are many outliers. These outlying samples contain many of the taxa, but in relatively low abundances. Overall, it is apparent that both the abundance and presence or absence of taxa accounts for the differences evident between weeks.

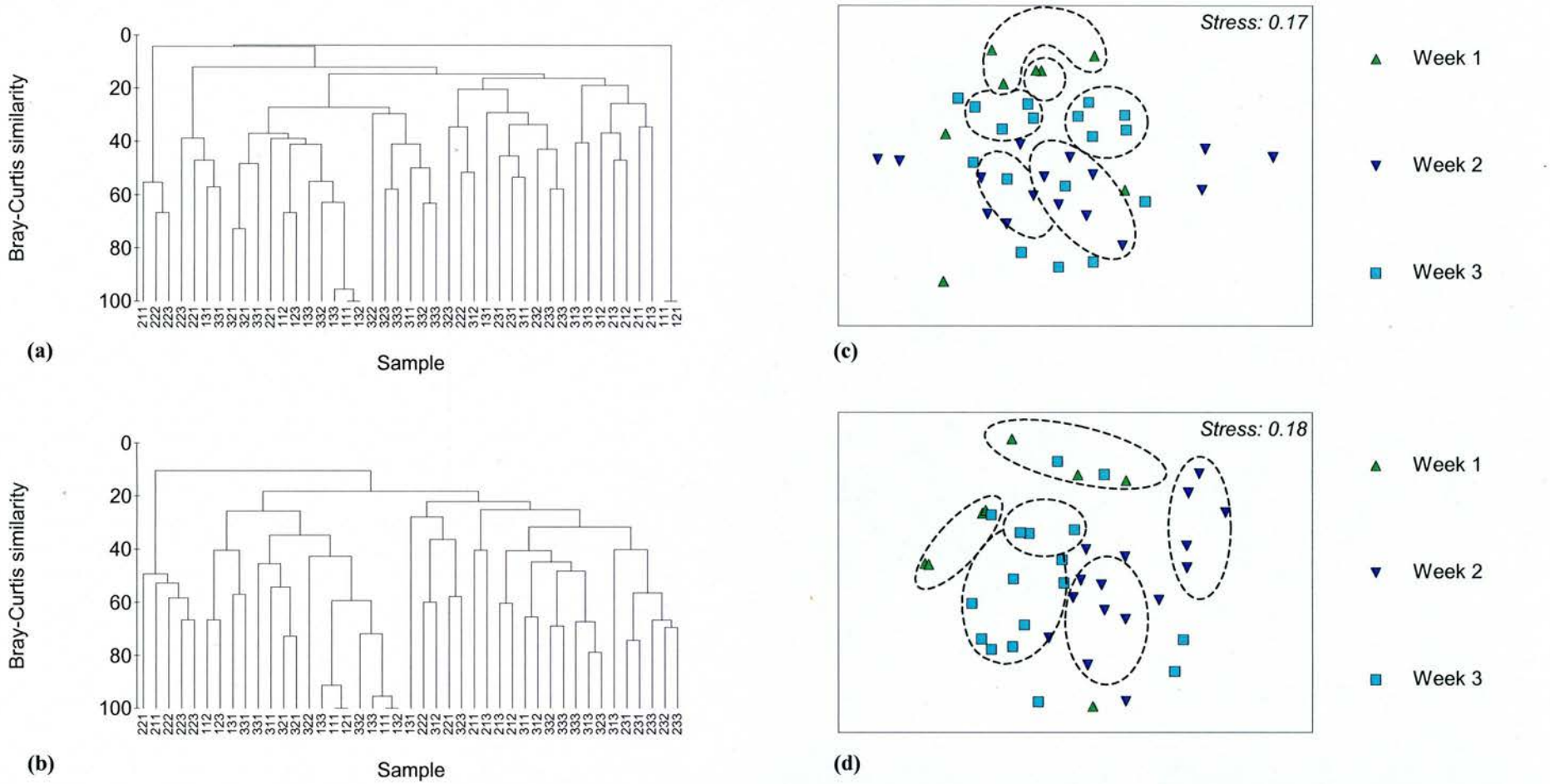


Figure 5.5. Dendrograms (a, b) for hierarchical clustering (group-average linking) and MDS ordination plots (c, d) of samples based on species (a, c) and family (b, d) composition. Dendrogram sample labels *jkl* represent week, day, hour, while MDS samples are pooled at the week level. Similarities in assemblages within weeks are apparent from clusters at 40 % similarity, superimposed on the MDS ordination plots as dashed lines.

Table 5.1. Larval taxa accounting for approximately two thirds of dissimilarity between groups of samples collected by light trap, based on CLUSTER analysis at 40 % Bray-Curtis similarity. Presence is denoted by *. Taxa present across all groups are marked † . The counts of *A.*stipes differ between weeks, those of *J.parvula* do not, indicating that the abundance of taxa as well as their presence or absence determines the clustering of samples.

Taxa	Week groups						Out-
	1	1	2	2	3	3	liers
Albula vulpes			*		*		*
Anchoa lamprotaenia			*		*		*
†*Atherinomorus stipes*	*	*	*	*	*	*	*
Blennioidei Type D				*		*	*
Blennioidei Type E				*		*	*
Carapus bermudensis			*				*
Coryphopterus sp			*	*		*	*
Doratonotus megalepis				*	*		*
Eucinostomus lefroyi	*		*				*
Gobiesox punctulatus		*	*	*		*	*
Gobionellus boleosoma			*				
Hypoplectrus sp			*	*			*
Jenkinsia lamprotaenia	*			*		*	*
†*Jenkinsia parvula*	*	*	*	*	*	*	*
Malacoctenus sp			*	*	*	*	*
Monacanthus setifer				*			*
Monacanthus sp						*	*
Pomacanthidae Type A				*		*	*
Scarus sp			*				*
Sparisoma sp			*			*	*
Syngnathidae Type A			*	*	*		

Key points

The key points of the temporal variation of larval supply assemblage composition may be summarised as:

- 39 taxa within 23 families were collected;
- week 2 shows the highest H' and d values;
- the median values of H' and d are significantly higher in week 2 than week 1;
- taxonomic composition of the assemblage varies significantly between weeks, and days nested within weeks, but not between hours nested within days and weeks;
- two thirds of the dissimilarity between samples grouped by weeks is accounted for by 21 taxa out of a possible total of 39;
- the abundance as well as the presence or absence of taxa accounts for differences between groups of samples.

5.3 *Discussion*

With regard to the two research questions posed at the start of the chapter, larval density and taxonomic composition are both significantly affected by temporal variability, mainly lunar periodicity, although this is hard to uncouple from tidal. Significant variation in total larval abundance was evident between the first week of sampling, during which the full moon occurred, and both the second and third weeks in which the three-quarter and new moon occurred, respectively. The reduction of larval collections during the full moon and increased larval abundances during the new and three-quarter moon phases are patterns observed in other light-trap studies (Doherty *et al.*, 1994; Thorrold *et al.*, 1994; Rooker *et al.*, 1996; Sponaugle & Cowen, 1996a, 1996b; Hickford & Schiel, 1999). The low abundances in week 1 collections are attributable to a lowered light attraction response and presumed increased predation pressure. Predation risk is often reduced during moonless nights (Rooker *et al.*, 1996; Hickford & Schiel, 1999). The greatest abundance of larvae in week 2 coincided with the three-quarter moon. No significant difference in larval abundance was evident between weeks 2 and 3, with the new moon occurring in the second night of week 3. Tidal effects are unlikely to account for the observed patterns in larval abundance, as weeks 1 and 3 saw high (spring) tides occurring in the middle of the sampling nights, whereas week 2 saw low (neap) tides during sampling periods.

A significant difference in larval abundance occurred between days within each week, indicating that variability was not solely due to lunar periodicity. Rather this suggests patchiness in larval distribution and indicates a need to sample for prolonged periods in order to gain an accurate picture of larval supply. No significant effect was evident due to the period of night at which sampling was conducted, indicating that peak larval abundance does not correspond with any particular time of night. However, the present study did not cover a full lunar cycle, and

a repeat study doing so is desirable to explain the observed patterns in larval abundance with more clarity.

The larval assemblage in all 3 weeks is predominated by larvae < 1.5 cm in length, indicating that the major proportion of the larval supply is newly hatched larvae. Only the size class of < 0.5 cm showed a significant temporal variation, between days nested within weeks. This again indicates patchiness in larval distribution and a need for prolonged sampling to accurately capture larval supply patterns.

Although it has rarely been cited as such, light intensity of light traps is likely to be a significant source of variation between different studies, in addition to factors such as geographic region, habitat, depth, time and trap-structure (Gehrke, 1994; Sponaugle & Cowen, 1996b). In addition, the taxonomic composition of light-trap collections is method dependent, primarily due to selectivity for positively phototaxic species. As there was no significant difference in the abundance of larvae collected by the two traps in the present study, it is assumed that their light intensity was comparable and therefore not a source of variation.

Lunar periodicity is evident when considering the number of species and families recorded for each week. These were, respectively, 11 and 9 in week 1 under a full moon, 36 and 22 in week 2 under a three-quarter moon, 29 and 19 in week 3 under a new moon. As may be expected from such figures, variation in species composition was significant between the first week, with the lowest overall larval abundance and number of species, and the second week, with the highest larval counts and species diversity. Week 3 is intermediate between the two and showed no significant difference in terms of species composition, despite containing almost triple the number of species and twice the number of families present the first week.

While the same general pattern is evident in the taxonomic composition of the three weeks as in the total larval counts, this is also true for the assemblage composition of the three days within each week, which differed significantly. As with the analysis of total larval counts, this indicates that variability is subject to other influences as well as lunar periodicity, such as patchiness in larval distribution due to larval pulses. In agreement with Doherty (1987) and Rooker *et al.* (1996), the present study indicates that monthly or quarterly sampling periods may miss some larval taxa and prolonged sampling periods are necessary in order to gain an accurate picture of larval.

The period of night at which sampling is conducted appears to be inconsequential, confirming assumptions of previous studies that peak larval abundance does not correspond with any particular time of night, and taxonomic composition of larval assemblages does not vary significantly (Holmes & O'Connor, 1988; Watson *et al.*, 2002). Although this removes the need for continuous sampling throughout the night, it is confounded by the apparent need for continuous sampling throughout entire lunar periods. It seems that there is an urgent need to assess both the short-term variability of light-traps over days and weeks, and long-term variability over more than two years.

Appendix 5.1. Relative abundance (%) of fish larvae species by hour, calculated as a percentage of individual species abundance pooled from both traps.

Family / order	Species / type	Week:	1									2										3									Number of individuals
		Day:	1			2			3			1			2			3			1			2			3				
		Hour:	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	
Achiriidae	*Achirus lineatus*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	1
Gobiesocidae	*Gobiesox punctulatus*		0	7.7	0	0	0	0	0	0	0	0	0	15.4	7.7	7.7	0	0	23.1	7.7	7.7	7.7	0	0	0	7.7	0	0	7.7	13
Albulidae	*Albula vulpes*		0	0	0	0	0	0	0	0	0	25.0	0	25.0	0	0	0	0	0	0	0	0	25.0	25.0	0	0	0	0	0	4
Engraulidae	*Anchoa lamprotaenia*		0	0	0	0	0	0	0	0	0	0	0	7.7	0	0	7.7	0	0	0	0	7.7	0	46.2	0	0	30.8	0	0	13
	Jenkinsia lamprotaenia		11.1	0	0	1.11	0	0	0	0	0	0	0	11.1	0	0	0	11.1	0	0	11.1	11.1	11.1	0	0	0	0	11.1	11.1	9
	Jenkinsia parvula		4.2	0	0	0	0	0	0	4.2	12.5	0	0	4.2	4.2	0	0	4.2	0	4.2	8.3	0	0	16.7	8.3	4.2	0	12.5	12.5	24
	Sardinella aurita		0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Atherinidae	*Atherinomorus stipes*		1.4	1.4	0	0	0	1.4	9.9	1.4	2.8	0	1.4	1.4	1.4	0	0	7.0	0	0	32.4	15.5	0	4.2	0	0	9.9	8.5	0	71
Gobiidae	*Bathygobius curacoa*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	1
	Coryphopterus sp		0	0	0	0	0	0	0	0	0	0	9.1	27.3	0	0	0	0	0	9.1	4.6	4.6	13.6	0	0	4.6	0	13.6	13.6	22
	Gobionellus boleosoma		0	0	0	0	0	0	0	0	0	0	42.9	42.9	0	0	0	0	0	7.1	0	7.1	0	0	0	0	0	0	0	14
	Gobiosoma sp		0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Blennioidei	Blennioidei Type D		0	0	0	0	0	0	22.6	0	0	0	3.2	0	3.2	0	0	22.6	19.4	25.8	0	0	0	0	0	0	0	3.2	0	31
	Blennioidei Type E		0	0	0	0	0	0	14.3	0	0	4.8	0	0	0	0	0	4.8	0	38.1	19.0	0	0	0	0	9.5	0	4.8	4.8	21
Carapidae	*Carapus bermudensis*		0	0	0	0	0	0	0	0	0	12.5	25.0	25.0	12.5	0	0	0	0	0	0	12.5	0	0	0	12.5	0	0	0	8
Scaridae	*Cryptotomus roseus*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25.0	0	0	50.0	0	0	0	0	0	25.0	4
	Scarus isertae		0	0	0	0	0	0	0	0	0	0	0	80.0	0	0	0	0	0	0	20.0	0	0	0	0	0	0	0	0	5
	Scarus sp		0	0	0	0	0	0	0	0	0	12.5	12.5	12.5	0	0	0	0	12.5	0	0	12.5	37.5	0	0	0	0	0	0	8
	Sparisoma sp		0	0	0	0	0	0	0	0	0	4.2	20.8	54.2	0	4.2	0	0	0	4.2	0	4.2	0	0	0	4.2	0	0	4.2	24
Labridae	*Doranotus megalepis*		0	0	0	0	0	0	12.5	0	0	0	0	25.0	0	0	0	37.5	0	0	12.5	0	0	12.5	0	0	0	0	0	8
	Halichoeres sp		0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Elopidae	*Elops saurus*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	1
Gerreidae	*Eucinostomus lefroyi*		0	0	0	0	0	0	0	0	0	0	35.7	28.6	7.1	0	0	7.1	14.3	0	0	0	0	0	0	0	0	7.1	0	14
Muraenidae	*Gymnothorax moringa*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	1
Serranidae	*Hypopletrus* sp		0	0	0	0	0	0	0	0	0	0	2.4	7.3	0	2.4	0	22.0	7.3	53.7	0	0	4.9	0	0	0	0	0	12.5	41
	Hypoplectrus unicolor		0	0	0	0	0	0	0	0	0	0	0	0	0	12.5	0	0	0	75.0	0	0	0	0	0	0	0	0	0	8
Labrisomidae	*Malacoctenus gilli*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	3
	Malacoctenus sp		0	0	0	0	0	0	2.6	0	0	0	0	0	0	2.6	0	15.8	0	18.4	36.8	5.3	0	13.2	2.6	0	0	0	0	38
Syngnathidae	*Bryx dunckeri*		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	1
	Syngnathidae Type A		0	0	0	0	0	0	0	0	0	6.7	0	6.7	0	0	0	0	26.7	46.7	6.7	0	0	0	0	0	6.7	0	0	15
Monacanthidae	*Monacanthus setifer*		0	0	0	0	0	0	5.9	0	0	0	0	0	20.6	20.6	2.9	8.8	2.9	11.8	14.7	8.8	0	0	0	0	2.9	0	0	34
	Monacanthus sp		0	0	0	0	0	0	0	0	0	22.2	22.2	0	0	11.1	11.1	11.1	0	0	22.2	0	0	0	0	0	0	0	0	9
Lutjanidae	*Ocyurus chrysurus*		0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Pomacanthidae	Pomacanthidae Type A		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5.4	10.8	75.7	0	0	5.4	0	2.7	0	0	0	0	37
	Pomacanthus arcuatus		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	1
Scorpaenidae	*Scorpaena* sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33.3	66.7	0	0	0	0	0	0	0	3
Tetraodontidae	*Sphoeroides maculatus*		0	0	0	0	0	0	50.0	0	0	0	0	0	50.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Pomacentridae	*Stegastes diencaeus*		0	0	0	0	0	0	25.0	0	0	0	25.0	0	0	25.0	0	0	0	0	0	25.0	0	0	0	0	0	0	0	4
	Stegastes sp		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	1
unidentified	unidentified Type M		0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
																														500

6.0 Recruitment limitation of fish in the mangrove habitat of a Caribbean island

6.1. *Introduction*

For reef fishes, larval supply and recruitment are both recognised as determining factors of the structure of adult populations (Caley *et al.*, 1996; Holbrook *et al.*, 2000; Fraschetti *et al.*, 2003). Most local populations of marine organisms are demographically open, with local recruitment uncoupled from local reproduction by a dispersed larval phase. Communities of marine species are often not in equilibrium, with their structure and dynamics dependent on the interactions of a suite of biotic and abiotic processes that affect both recruitment and post-recruitment survival. Recruitment to open marine populations is generally defined as the addition of individuals to local populations following settlement from the pelagic larval phase to the benthic or demersal early juvenile phase.

Much of the reputation of mangroves as an important nursery site comes from the presence of pre-recruits (i.e. larval or early juvenile stages) within the mangroves, the adult stages often being found in different habitats. Such populations, which have survived the highly vulnerable egg and yolk sac phases of early life, are often used as an indicator of adult populations, and fluctuations are generally associated with a reduction in spawning biomass. In order to validate this assumption it is necessary to assess the extent to which variation in the size of populations is due to variation in the influx of young or recruiting organisms.

The research questions addressed are:

1. Is the larval supply related to the juvenile assemblage?
2. Is recruitment related to spawning (adult) stock in mangrove fish populations?

6.2. *Results*

6.2.1. Comparison of larval, juvenile and adult abundance

Under the assumption that larval abundance of the seagrass represents the supply to the larval population of the mangroves, the counts of larvae collected by light trap in the two habitats are expected to correlate, with no significant difference between their means. As variation between the overall mean larval population and supply is insignificant, the former should reflect the latter (Two sample T-test: $T = 1.51$, $p = 0.130$).

The mangrove and seagrass larval abundance show similar patterns of temporal variation, with the larval supply generally exceeding the larval population (see Figure 4.6). Direct comparison by date shows no significant correlation between the mangrove and seagrass counts (Pearson correlation: $r = 0.451$, $p = 0.141$). However, a significant correlation is evident when a lag phase of one sampling interval is imposed between the collection dates of larval population and supply (Pearson correlation: $r = 0.967$, $p \leq 0.001$). The abundance of the larval population therefore reflects the larval supply of the previous sampling date. This indicates a lag phase of approximately 2 to 4 weeks between larval supply to and settlement in the mangroves.

Variation by Region

Both the larval population of the mangroves and the larval supply of the seagrass show significant variation between the temporal patterns of Calabash Cay as a whole, and those of each Region. Patchiness in larval distribution is apparent at this finer spatial scale, with the temporal variation of the mangrove larval population in Regions 1 and 2 agreeing with that of Calabash Cay as a whole, while that of Region 3 does not (Pearson correlation: $r = 0.895$, $p \leq 0.001$; $r = 0.598$, $p = 0.040$; $r = 0.359$, $p = 0.251$ respectively). In contrast, only the larval

supply of Region 3 corresponds with that of the whole cay (Pearson correlation: $r = 0.977$, $p \leq 0.001$). Additional reinforcement of patchy larval distribution is evident from the strong positive correlation between the larval population and supply within all the Regions (Pearson correlation: $r \geq 0.727$, $p \leq 0.007$), directly contrasting with the observations made for the overall larval distribution in which correlation was only evident with a time lag of one sampling interval. Multivariate analysis confirms that significant variation in larval counts is apparent between sampling dates but not habitat type (Balanced ANOVA: $F = 5.15$, $p \leq 0.001$; $F = 0.68$, $p = 0.412$ respectively).

All three Regions show a strong positive correlation between the larval population of the mangroves and the supply from the seagrass beds, and the same pattern is expected at the level of Stations. Although this is apparent for Region 1, in Region 2 there is no correlation between the larval population and supply of either Station D or F, while in Region 3 the same is true of Stations G and I (Pearson correlation: $r = 0.016 - 0.460$, $p = 0.960 - 0.132$). Nevertheless, the extent of variation due to sampling date remains significant whereas habitat is not a significant factor (Balanced ANOVA: $F = 10.10$, $p \leq 0.001$; $F = 1.35$, $p = 0.247$ respectively).

Larval distribution patterns exhibited by the plankton net tows are similar to those described by the nocturnal collections, displaying a similar discrepancy between the mangrove and seagrass larval densities. This suggests that differences in the temporal patterns detected by the two methodologies are due to diel variation in larval distribution, as well as collection method.

In the day larval collections, the overall mean larval density for the mangrove population is significantly lower than the mean larval count in the seagrass (Two sample T-test: $T = -6.72$, $p \leq 0.001$). With the exception of the final sampling date of 05/11/2001, the larval supply

consistently exceeds the larval population, implying a high larval supply to, but a low larval retention in, the mangroves. However, no significant correlation is evident, even with the introduction of lag phases of one or more sampling intervals (Pearson correlation: $r = 0.513$, $p = 0.088$; $r = 0.115$, $p = 0.721$ respectively).

The lack of significant correlation between larval supply and population on the same sampling dates indicates a significant difference in their mean densities. The larval density of the seagrass is significantly greater than that of the mangroves on 3 of the 12 sampling dates: 03/08/2000, 09/07/2001 and 25/08/2001 ($T = -2.50$, $p = 0.037$; $T = -3.53$, $p = 0.003$; $T = -3.72$, $p = 0.006$, respectively). The first date occurs during the 1st quarter of the lunar cycle immediately after the new moon, when a high larval influx is expected. The remaining two dates coincide with the light trap collection dates on which the larval population was significantly greater than larval supply. The reversal of larval distribution patterns between the collections made by plankton net during the day and light trap at night indicate a diel variation, with larvae residing in the seagrass during the day and migrating to the mangroves at night.

As seen with the light trap counts, weak correlation between the mangrove and seagrass densities collected by plankton net shows patchiness within each Region (Pearson correlation: $r = -0.112 - 0.050$, $p = 1.26 - 0.877$). The difference in temporal patterns of larval population and supply is confirmed by multivariate analysis of date and habitat, both of which are significant factors (Balanced ANOVA: $F = 2.13$, $p = 0.042$; $F = 16.83$, $p \leq 0.001$ respectively).

Despite temporal and spatial patchiness in larval distribution, there is apparent correlation between the overall density of the larval supply to and the larval population within the mangroves. As the larval population of the mangroves is expected to be related to the subsequent

juvenile abundance, so is the larval supply. Many juvenile reef fish show active diel migration between habitats, with the day seagrass assemblage reflecting the mangrove assemblage at night, and vice versa. Comparison of the larval supply and population to the mangrove and seagrass juvenile assemblages is therefore valid.

The density of the juvenile assemblage (see Figure 4.7) shows significant temporal variation in the mangroves, but not in the seagrass (One-way ANOVA: $F = 4.00$, $p = 0.003$; $F = 2.31$, $p = 0.054$ respectively). When compared directly by date, the mangrove and seagrass counts show no significant correlation (Pearson correlation: $r = -0.469$, $p = 1.71$). Comparison of the mean counts per survey date for each habitat within each Region shows habitat is not a significant factor in Regions 1 and 3, but is significant in Region 2 (Balanced ANOVA: $F = 3.89$, $p = 0.057$; $F = 0.09$, $p = 0.761$; $F = 15.47$, $p \leq 0.001$ respectively).

The survey dates for larvae, juveniles and adults do not always coincide as each method required a whole day or night, and equipment failure or bad weather resulted in only 5 sets of dates ("date groups") during which all methods were used (see Figures 4.6 and 4.7). Therefore all comparative analysis is performed on the 5 date groups in question, which occur at the end of June, July, August, September and October.

Comparison of temporal variation in abundance of each stage shows that variation in the larval mangrove population reflects the adult seagrass density with a time lag of 2 months, and corresponds directly to the adult mangrove density (Pearson correlation: $r = 0.794$, $p = 0.011$; $r = 0.756$, $p = 0.018$ respectively). The adult mangrove density lags behind the adult seagrass density by 1 month (Pearson correlation: $r = 0.736$, $p = 0.024$). The total juvenile density in turn reflects the larval supply, also with a 2-month lag (Pearson correlation: $r = -0.823$,

p = 0.006). This indicates a general movement of the adult assemblage across or directly from the seagrass into the mangroves, where an increase in larval production occurs with increasing adult abundance and a subsequent increase in juvenile densities. The increase in juvenile densities in the seagrass is followed by an increase in adult density, with a lag of 1 month (Pearson correlation: r = 0.704, p = 0.034).

Species-specific patterns

During the 2001 sampling season 10 taxa were recorded as larvae and juveniles in the seagrass and mangrove habitats (Appendix 3.1): *Atherinomorus stipes*, Clupeidae Type A, *Cryptotomus roseus*, *Halichoeres* sp., *Hypoplectrus unicolor*, *Monacanthus* sp., *Ocyurus chrysurus*, *Scarus* sp., *Sparisoma* sp. and *Strongylura notata*. Juveniles and adults of many species exhibit diel migration between habitats, as shown by *O.chrysurus* juveniles, the abundance of which in the mangroves corresponds directly with the density in the seagrass beds (Pearson correlation: r = 0.949, p = 0.014). As a result comparison between and across both habitats is appropriate.

A significant correlation between the monthly larval and juvenile abundance of both *Halichoeres* sp. and *S.notata* is apparent in the mangroves (Pearson correlation: r = 0.970, p = 0.006; r = 0.880, p = 0.049 respectively). Although this indicates a relationship between the settlement and recruitment of *Halichoeres* sp. and *S.notata*, it does not illustrate whether their larvae are entering the mangroves from elsewhere. The density of adult *Halichoeres* sp. in the seagrass corresponds directly with the seagrass juvenile abundance, and with the mangrove larval abundance with a time lag of one month (Cross-correlation: r = 0.935, p = 0.020; r = 0.950, p = 0.013 respectively). This suggests the adult seagrass population is supplying larvae that settle into the mangrove habitat and are recruited into the mangrove population, then migrates back to the seagrass beds.

For *Scarus* sp. the larval supply and recruitment to the mangroves is related to the adult stock of both the mangrove and seagrass habitats. The adult abundance of *Scarus* sp. in both habitats corresponds with its larval density in the seagrass, with a time lag of 1 month, and directly with juvenile abundance in the mangroves (Cross-correlation: $r \geq 0.897$, $p \leq 0.039$). A significant correlation between the larval and juvenile abundance is apparent across the two habitats (Cross-correlation: $r = 0.880$, $p = 0.049$).

The scarid *Cryptotomus roseus* shows significant correlation between the seagrass larval supply and the mangrove juvenile population, with a time lag of 2 months (Cross-correlation; $r = 0.900$, $p = 0.037$). The same relationship is apparent between the larval supply and the abundance of adults in both habitats, while the mangrove adult and juvenile populations show a direct correspondence in density (Cross-correlation: $r \geq 0.900$, $p \leq 0.037$). This suggests that larvae are supplied from an external source, settle in the mangroves and develop into juveniles and adults. The resulting adult population is then distributed over both habitats.

In the seagrass *Hypoplectrus unicolor* shows a significant correlation between the larval density and juvenile abundance 2 months later (Cross-correlation: $r = 0.882$, $p = 0.048$). The same relationship is evident between the larval supply and the adult mangrove population (Cross-correlation: $r = 0.900$, $p = 0.037$). When amalgamated with larvae and juveniles identified to the level of genus, a significant correlation between the seagrass larval supply and the mangrove juvenile population is evident, with a time lag of 1 month (Cross-correlation; $r = 0.900$, $p = 0.037$). The adult mangrove density lags behind the juvenile abundance by a month also (Cross-correlation: $r = 0.950$, $p = 0.013$). This indicates that *Hypoplectrus* larvae are supplied via the seagrass, and juveniles are then recruited into the mangroves,

where some develop into adults. Migration to the seagrass beds then occurs, as juveniles or adults.

Amalgamating taxa to the level of family, Carangidae, Chaetodontidae, Gerreidae and Pomacentridae were recorded as larvae and juveniles in 2001 in addition to Atherinidae, Belonidae, Clupeidae, Labridae, Lutjanidae, Monacanthidae, Scaridae and Serranidae. At this level, the correspondence between larvae and juveniles in the mangroves shown by *Strongylura notata* is still evident for the family Belonidae. Of the remainder, only the Chaetodontidae exhibit any significant correlation. The mangrove adult population density corresponds with the larval density a month later (Cross-correlation: $r = 0.881$, $p = 0.048$). Variation in the mangrove larval population is in turn reflected by the seagrass juvenile and adult densities with a lag of 1 month (Cross-correlation: $r = 0.950$, $p = 0.013$). The seagrass adult and juvenile abundances show a direct correspondence (Cross-correlation: $r = 0.999$, $p \leq 0.001$). Therefore chaetodontid spawning appears to occur in the mangroves, with subsequent settlement and recruitment into the seagrass beds. The same pattern is not clearly discernible without the larval collections, requiring an assumption that the adult mangrove population is related to the juveniles and adults of the seagrass beds.

However, association between just two developmental stages does indicate relationships for some taxa, at the levels of species, genus or family. Across both habitats, the larval density of the lutjanid *Ocyurus chrysurus* lags behind the adult abundance by a month (Cross-correlation: $r = 0.958$, $p = 0.010$). Another scarid genus, *Sparisoma*, shows a direct correlation between the seagrass adult density and larval supply (Cross-correlation: $r = 0.998$, $p \leq 0.001$). Amalgamation of all the scarid genera shows a correlation between the adult mangrove population and the larval density in the seagrass with a time lag of 1 month (Cross-correlation: $r = 0.881$, $p = 0.049$). In these cases it appears that a local adult population produces the larvae. Interpreting

relationships from the distribution of adults and juveniles is less clear-cut, as shoals often consist of a mixture of the two stages. This probably accounts for the direct correlation in abundance between juveniles and adults of *Eucinostomus argenteus* and *Lutjanus mahogoni* in the mangroves, and *Haemulon sciurus* and *Eucinostomus jonesi* in the seagrass (Cross-correlation: $r \geq 0.896$, $p \leq 0.039$).

Key points

The relationship of larval, juvenile and adult assemblages in terms of overall abundance can be summarised as:

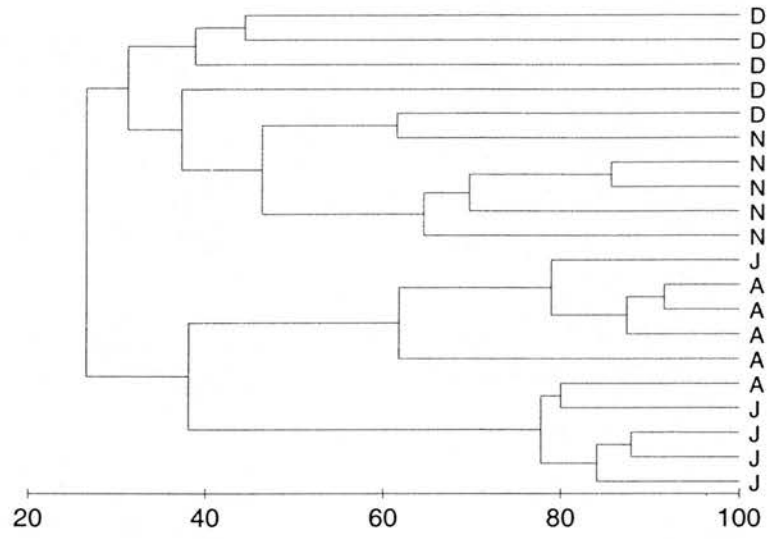
- the mangrove larval population reflects the adult seagrass density with a time lag of 2 months, and corresponds directly to the adult mangrove abundance;
- the overall density of the adult mangrove assemblage lags behind the seagrass adult density by 1 month;
- the overall mangrove larval population reflects the larval supply from the seagrass beds with a lag phase of 2 to 4 weeks, with significant temporal variation apparent for both;
- within each Region the density of the larval supply corresponds directly with the mangrove larval population, but this is not always evident within Stations;
- diel variation in larval distribution is apparent, with movement apparent from the seagrass to the mangroves at night;
- the juvenile mangrove and seagrass densities do not correspond, with only the former showing significant temporal variation;
- overall juvenile density reflects the larval supply with a two month lag period;
- in the seagrass beds, adult density reflects the juvenile abundance with a lag of 1 month.

Clearer relationships between the different life stages are apparent for specific taxa, and can be summarised as:

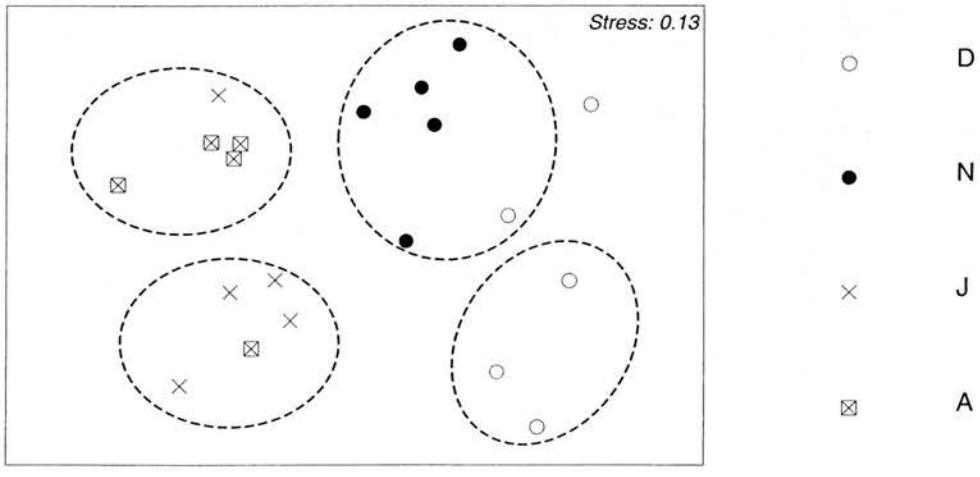
- settlement and recruitment of *Strongylura notata* to the mangrove habitat is evident;
- *Halichoeres* sp. larvae produced by a seagrass population settle and recruit into the mangroves, but migrate back to the seagrass beds;
- the larval supply of *Scarus* sp. and recruitment to the mangroves is related to adult stock in both habitats;
- *Cryptotomus roseus* and *Hypoplectrus* sp. larvae appear to be recruited to the mangroves from an external source, subsequently migrating to seagrass as adults, or juveniles in the latter case;
- larvae of the family Chaetodontidae appear in the mangroves, with subsequent settlement and recruitment into the seagrass beds;
- the larvae of *Ocyurus chrysurus*, *Sparisoma* sp. and scarids in general appear to be produced by a local adult population.

6.2.2. Comparison of larval, juvenile and adult assemblage composition

Based on presence/absence of taxa, the reef fish of Calabash Cay show a relatively strong grouping into the three life history stages, with the larval assemblage further grouped according to night and day collections (Figure 6.1). An analysis of similarities shows a significant difference between the presence/absence composition, at both species and family level, of the four life history stage groups (1-way ANOSIM: $R = 0.774$, $p \leq 0.001$; $R = 0.677$, $p \leq 0.001$ respectively). Approximately two thirds of the dissimilarity between the life history groups is accounted for by the presence or absence of 52 taxa, out of a possible 92 (Table 6.1).



(a)



(b)

Figure 6.1. Dendrogram (a) for hierarchical clustering (group-average linking) and non-metric MDS ordination plot (b) of life history stages based on presence/absence of taxa in night (N) and day (D) larval assemblages, and juvenile (J) and adult (A) assemblages recorded for 5 date groups. Dashed lines represent cluster groupings at a similarity level of 40 %. Strong grouping into the respective life stages is evident at 40 % similarity, indicating that distinctive changes in taxonomic composition occur between each stage.

Table 6.1. Taxa accounting for approximately two thirds of dissimilarity between life history groups, based on CLUSTER analysis at 40 % Bray-Curtis similarity. Presence is denoted by *. Groups are predominated by night (N) and day (D) larval, juvenile (J) and adult (A) collections.

Taxa	Life-history Group				
	N	D	J	A	Outlier
Abudefduf saxatilis			*	*	
Acanthurus coeruleus			*	*	
Acanthurus sp			*	*	
Achirus lineatus		*			
Anisotremus virginicus				*	
Atherinomorus stipes					
Bathygobius curacao	*				*
Blennioidei Type D	*				
Brevoortia sp	*	*			
Chaetodon capistratus			*	*	
Chaetodon sp			*	*	
Clupeidae Type A	*		*		
Cryptotomus roseus			*	*	
Diodon sp			*		
Eucinostomus argenteus			*	*	
Eucinostomus lefroyi	*	*			
Eugerres plumieri	*				
Gerres cinereus			*	*	
Gerreidae Type A					
Gobiesox punctulatus	*	*			
Gobiidae Type A	*		*	*	
Gobiosoma sp	*				
Haemulon flavolineatum			*	*	
Haemulon plumieri			*	*	
Haemulon sciurus			*	*	
Halichoeres sp	*		*	*	
Hypoplectrus sp	*				
Hypoplectrus unicolor			*	*	
Jenkinsia lamprotaenia	*				
Jenkinsia parvula	*				
Lutjanus apodus			*	*	
Lutjanus griseus			*	*	
Lutjanus jocu			*	*	
Lutjanus mahogoni			*	*	
Lycengraulis grossidens	*				
Malacoctenus sp	*				
Microgmathus sp		*			
Monacanthus sp	*				*
Nes longus	*				
Ocyurus chrysurus			*	*	
Pseudupeneus maculatus			*		
Pomacanthidae Type A	*			*	
Pomacentridae Type A			*	*	
Scarus sp			*	*	
Scorpaena sp	*	*			
Sparisoma radians	*				
Sparisoma sp			*	*	
Sphoeroides maculatus		*			
Sphyraena barracuda			*	*	
Strongylura notata			*	*	
Syngnathidae Type A					
Tripterygiidae Type A	*				

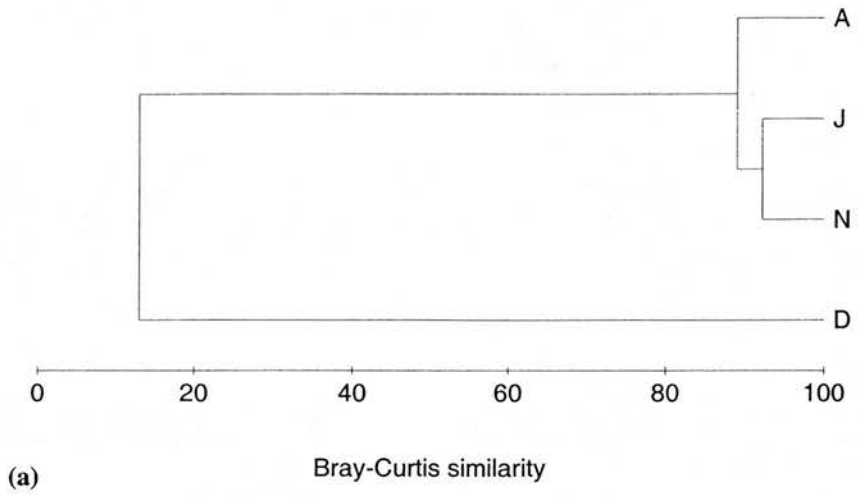
A significant difference between each group pairing is evident from pairwise tests, with the exception of the juvenile and adult assemblages at the family level (1-way ANOSIM: $R = 0.258$, $p = 0.127$). The occurrence of many taxa in mixed shoals of juvenile and adult stages probably accounts for this. An analysis of similarities on the assemblages grouped by the months of June, July, August, September and October shows no significant difference between the overall taxonomic composition of each month, at either the species or family level (1-way ANOSIM: $R = -0.173$, $p = 0.979$; $R = -0.185$, $p = 0.975$ respectively).

All four groups covering the three life history stages show a significant variation in assemblage composition with time when analysed individually (ANOSIM: $R \geq 0.069$, $p \leq 0.027$). Therefore it is of interest to investigate whether the variations with time of the groups are linked. Comparison of all rank correlation coefficients between all pairs of similarity matrices, groups the adult, juvenile and night larval assemblages together at a similarity level of approximately 90 %, with the rank correlation of the day larval assemblage lying outside at a similarity level of approximately 15 % (Figure 6.2). The similarity between the adult, juvenile and night larval assemblage rank correlation coefficients, suggests that the taxonomic composition of each assemblage follows a similar pattern with time. The dissimilarity of the day larval assemblage reflects the patchy spatial distribution of larvae in the water column.

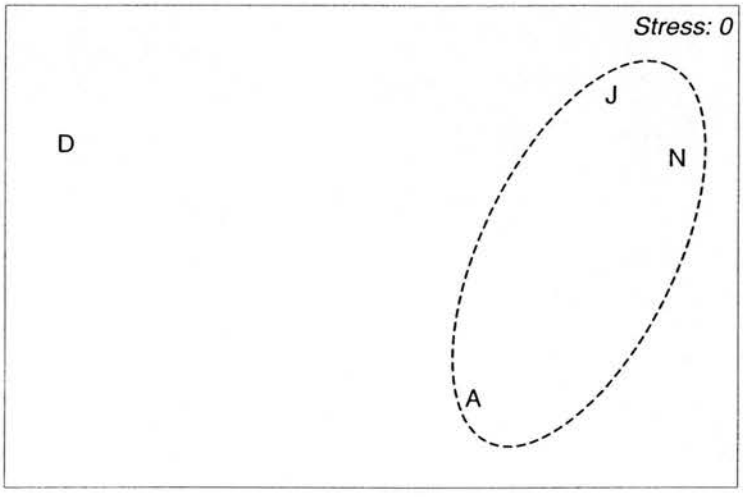
Key points

The relationship of the larval, juvenile and adult assemblages in terms of overall taxonomic composition can be summarised as:

- the larval, juvenile and adult reef fish assemblages differ significantly in composition when compared by month;
- the presence/absence of 52 taxa account for two thirds of dissimilarity between the respective life stage assemblages;



(a)



(b)

Figure 6.2. Dendrogram (a) for hierarchical clustering (group-average linking) and 2nd stage non-metric MDS ordination plot (b) of rank correlation coefficients of night (N) and day (D) larval, juvenile (J) and adult (A) assemblages recorded for 5 date groups. Dashed line represents cluster grouping at a similarity level of approximately 90 %, showing a strong correlation between the temporal variation in taxonomic composition of the night larval, juvenile and adult assemblages.

- no significant temporal variation in overall taxonomic composition is apparent;
- the taxonomic compositions of the adult, juvenile and night larval assemblages follow a similar pattern with time.

6.3. *Discussion*

6.3.1. Influence of larval supply

The density of the juvenile assemblage shows significant temporal variation in the mangroves but not in the seagrass, indicating an overall movement of transient individuals in the mangrove habitat. Such movement between habitats during single life-cycle stages is a common phenomenon for many fish species (Yàñez-Arancibia *et al.*, 1988; Cochere de la Morinière *et al.*, in press). However, migration may be more visible in the mangrove habitat, as larger individuals predominate and the structure is more amenable to visual census techniques.

Small-scale larval patchiness is apparent between the two habitats on a scale of 100s of metres, but not at 1 km, showing the importance of sampling on various spatial scales. Similarly, a wide timescale of sampling is required as reproduction in tropical waters is generally continuous, with peaks occurring at certain times of the year. The timescale of the present study covers the peak reproductive periods known for most Caribbean reef fish species (Carter & Perrine, 1994; García-Cagide *et al.*, 2001; Serafy *et al.*, in press).

For the purposes of the present study, the seagrass larval assemblage is taken to represent the larval supply to the mangroves. The density of the larval supply generally exceeds that of the mangrove larval population, although not always significantly. Both show significant variation with time, however, indicating the occurrence of larval pulses. A lag phase of 2 to 4 weeks between the two indicates a large

proportion of larvae are entering the mangroves via the seagrass. This suggests that larvae are being produced by spawning stock in the seagrass beds. However, as most coral reef fish are pelagic spawners (Richards & Lindeman, 1987; Doherty & Williams, 1988), the majority of the larvae are probably being carried over the seagrass from the outer reef of the atoll. The occurrence of time lags in the density distributions of adults and larvae between the two habitats also suggests a general movement of adults from the seagrass to the mangroves to spawn. This in turn indicates that there is some local input to the mangrove larval population.

Lag periods between the densities of the three life stages under consideration indicate larvae are initially supplied to the mangroves, settle to the seagrass and move to the mangroves as juveniles to develop into adults before migrating to the coral reefs. In answer to the first of the research questions posed, the juvenile assemblage does appear to be related to the larval supply in terms of absolute abundance. When looking at individual species and types, a clear relationship between the seagrass larval supply and the mangrove juvenile population is evident for the serranid *Hypoplectrus* sp. and the scarid *Cryptotomus roseus*. *Hypoplectrus* sp. larvae then appear to migrate back to the seagrass as juveniles, whereas *C.roseus* complete their development to adults before leaving the mangrove habitat.

The relationship between larval supply and juvenile mangrove populations is less clear-cut for other taxa. For example, settlement and recruitment of *Strongylura notata* to the mangrove habitat is evident, but does not appear to be related to larval assemblage in the seagrass beds, suggesting larvae are produced locally. The larvae of *Halichoeres* sp. also appear to settle and recruit into the mangroves, although this is followed by migration to an adult population in the seagrass beds, which potentially constitutes the spawning stock.

The second research question asks whether recruitment is related to the adult spawning stock in mangroves. The answer is positive for some taxa, and shown most clearly by *Scarus* sp., for which the larval supply and recruitment to the mangroves is related to adult stock in both habitats. Larvae and adults of the family Chaetodontidae occur in the mangroves, with subsequent juvenile settlement and recruitment into the seagrass beds apparent. The larvae of *Ocyurus chrysurus*, and scarids such as *Sparisoma* sp. are correlated with local adult populations across both habitats. Although *O.chrysurus* settlement to mangroves has been reported elsewhere, they are also known residents of seagrass beds (Dennis, 1992, Lindeman *et al.* 1998; Valdés-Muñoz & Mochek, 2001).

Larval supply and recruitment are generally considered to be determinants of adult fish populations (Heath, 1992; Caley *et al.*, 1996; Holbrook *et al.*, 2000; Fraschetti *et al.*, 2003), and the apparent regulation of the juvenile and adult populations by larval supply implies recruitment limitation is being exercised to some extent in the mangroves of Calabash Cay. Although most local populations are considered to be open, a marked proportion of the settling cohort may consist of self-recruiting larvae (Jones *et al.*, 1999; Swearer *et al.*, 1999). This is evidenced by the apparent relationship in several taxa between recruitment and adult spawning stock in the mangroves/seagrass/both. Some migration between habitats prior to spawning is evident, and Chapter 7 examines the movement patterns of the larval, juvenile and adult life stages further.

7.0 Ontogenetic migration between seagrass and mangrove habitats within a Caribbean atoll

7.1. *Introduction*

Fish may migrate between adjacent shallow water habitats due to feeding, spawning or ontogenetic behaviour, and so provide links between spatially separated communities. In the Caribbean, the function of seagrass beds and mangroves as nursery habitats for reef fish has been generally accepted (Parrish, 1989). Juveniles in nursery habitats are considered to be spatially separated from adults, with subsequent (ontogenetic) migration from the nursery to habitats occupied by adults occurring over a specific size range.

The timing of such ontogenetic migrations are related to changes during the life-cycle of the fish, such as gradients or seasonal changes in environmental factors, physiological or morphological changes in juveniles, changes in diet or food distribution, and outgrowing a structurally complex habitat. Quantitative data on ontogenetic shifts in habitat use from nursery to adult habitat association are largely lacking (Rooker & Dennis, 1991; Nagelkerken *et al.*, 2000b) and the relative importance of nurseries to different size-classes of reef fish species is poorly known (Birkeland, 1985). To alleviate size-related competition, individual species may use different migration patterns, and may show a strong association with either mangrove or seagrass beds where the two are in close association. The research questions to be addressed here are:

1. Do reef fish taxa display any preference for mangrove or seagrass habitats during the larval, juvenile and adult life stages?
2. How influential is the temporal variation in environmental variables on the assemblage composition of larval reef fish in the mangrove and seagrass habitats?

7.2. *Results*

7.2.1. Variation in taxonomic composition of larval, juvenile and adult assemblages between habitats

The nocturnal larval reef fish assemblage of the seagrass habitat has a significantly higher mean Shannon diversity index (H') value than that of the mangroves (T-test: T = -2.22, p = 0.027), reflecting the greater abundance and species richness of the former (Table 7.1). Although the H' value of the day larval assemblage is also greater in the seagrass, the difference is not significant (T-test: T = -1.59, p = 0.114). The adult and juvenile assemblages show a higher diversity in the mangrove habitat, but again the difference is not significant (T-test: $T \leq 1.91$, $p \geq 0.059$). This indicates that although the proportion of species present as larvae, and therefore available to settle, is greater in the seagrass than in the mangroves, a larger proportion of taxa are recruited into the mangrove rather than the seagrass assemblages.

Table 7.1. Mean Shannon diversity index (H') values ± standard error of larval, juvenile and adult assemblages in the mangrove and seagrass habitats of Calabash Cay. The mean H' value of the night mangrove larval assemblage is significantly lower than that of the seagrass assemblage *($p < 0.05$). The juvenile, adult and day larval assemblages both have a higher mean H' value in the mangroves than the seagrass, although the difference is not significant.

	Habitat	
	Mangrove	Seagrass
Species diversity:		
Larval (night)*	0.35 (0.04)	0.49 (0.05)
(day)	0.06 (0.02)	0.11 (0.02)
Juvenile	1.15 (0.08)	0.94 (0.07)
Adult	0.77 (0.09)	0.61 (0.06)

The only variation in H' value apparent within either habitat is shown by the juvenile and adult assemblages, both of which show a significant difference in H' value with Region in the seagrass beds (ANOVA: F = 5.63, p = 0.007; F = 3.69, p = 0.034 respectively). The juvenile seagrass assemblage has a significantly higher mean H' value in

Region 3 than Region 1, while the adult seagrass assemblage has a significantly higher mean H' value in Regions 1 and 3 than Region 2. By contrast, the highest mean H' value of larval supply is in Region 1, and the lowest value in Region 2. The high adult diversity of Region 1 is therefore reflected by the larval supply, and of Region 3 by the juvenile seagrass assemblage. In turn, the low juvenile diversity of Region 1 corresponds with a high larval diversity.

The juvenile seagrass assemblage also shows a significant temporal variation in diversity, with a significant difference between the lowest mean H' value in June and the highest, in September (ANOVA: $F = 2.45$, $p = 0.043$). Therefore new juvenile taxa are entering the seagrass assemblage over the three-month period, with a peak in diversity in September. There is no significant correlation evident between the mean H' values of each habitat for the larval, juvenile and adult assemblages, either by date, Region or Station (Pearson correlation: $r \leq 0.761$, $p \geq 0.377$). This implies that the increase in juvenile taxa in the seagrass is due to recruitment into the seagrass beds, rather than migration from adjoining mangrove habitat.

A more detailed multivariate examination of community structure using non-metric multi-dimensional scaling (MDS) shows a clear separation of mangrove and seagrass communities for each assemblage (Figure 7.1). Despite this, and the significant difference in the mean Shannon diversity values, the composition of the mangrove and seagrass night larval assemblages does not differ significantly at either species or family level (ANOSIM: $R = 0.021$, $p = 0.083$; $R = 0.018$, $p = 0.197$ respectively). The adult, juvenile and day larval assemblages all show significant differences in taxonomic composition between the two habitats, however (ANOSIM: $R \geq 0.223$, $p \leq 0.001$). Comparison of the mangrove and seagrass assemblages of each stage by SIMPER shows that two thirds of the dissimilarity is due to 11 out of 36 taxa for

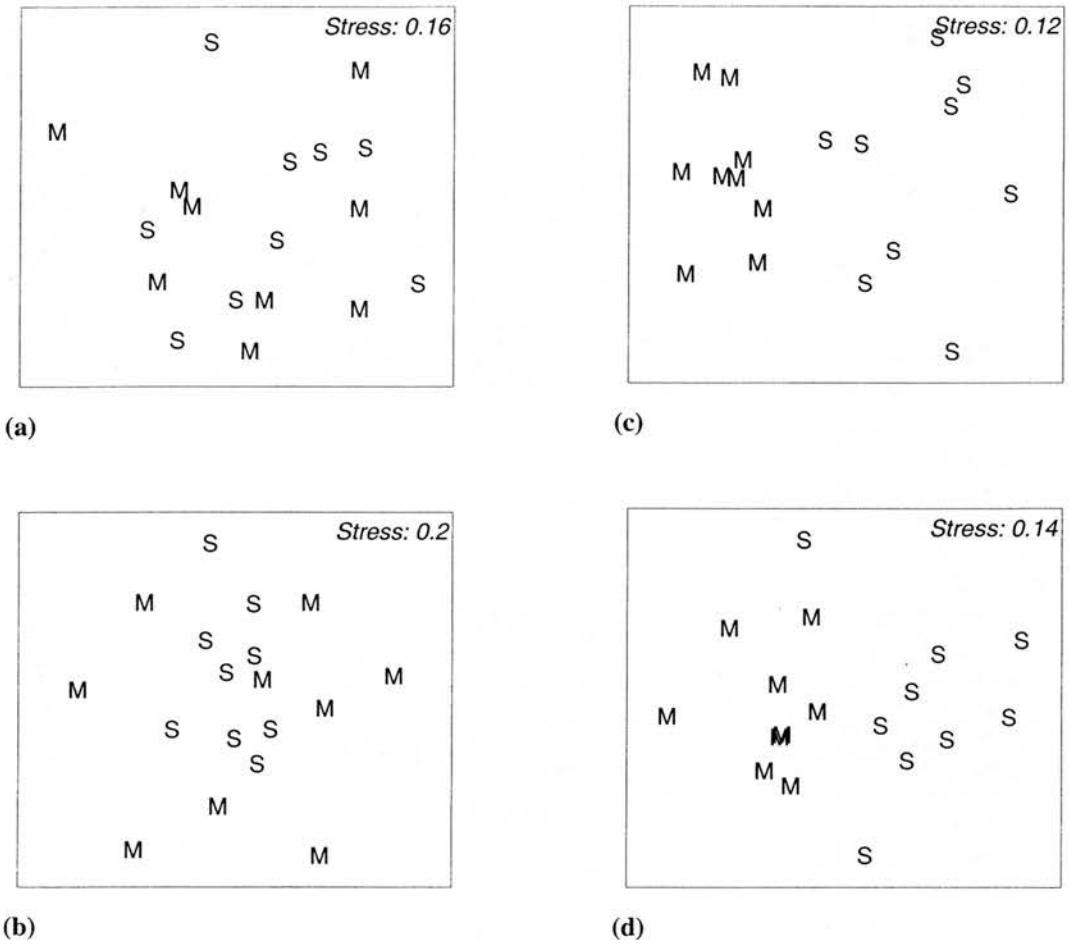


Figure 7.1. MDS ordination plots for (a) night larval, (b) day larval, (c) juvenile and (d) adult assemblages in the mangrove (M) and seagrass (S) habitats. Variation in assemblage composition with habitat is evident for all life stages, and a clear separation between the two habitats is apparent for the juvenile and adult assemblages.

adults, to 20 out of 50 taxa for juveniles, and to 7 out of 39 taxa for day larval collections (Table 7.2).

For the adult assemblage, all 11 taxa are present in both habitats with the exception of *Atherinomorus stipes*, *Haemulon flavolineatum* and *Lutjanus apodus*, which are only present in the mangrove adult assemblages. For the juvenile assemblage, all 20 species are present in both habitats with the exception of *Atherinomorus stipes* and *Lutjanus jocu*, which are only present in the mangroves, and *Eucinostomus jonesi* and *Pseudupeneus maculatus* present only in the seagrass beds.

Similarly, all except 1 of the 7 day larval taxa, Sparidae Type A, are present in both habitats.

Table 7.2. Adult, juvenile and day larval taxa accounting for approximately two thirds of dissimilarity between clustered mangrove (M) and seagrass (S) assemblages, grouped at 65 % Bray-Curtis similarity. * denotes presence.

Taxa	Adult		Juvenile		Larval (day)	
	M	S	M	S	M	S
Abudefduf saxatilis			*	*		
Acanthurus sp			*	*		
Atherinomorus stipes	*		*		*	*
Brevoortia sp.					*	*
Clupeidae Type A			*			
Chaetodon capistratus			*	*		
Eucinostomus argenteus	*	*	*	*		
Eucinostomus jonesi				*		
Eucinostomus lefroyi					*	*
Gobiidae Type A	*	*				
Gobiesox punctulatus					*	*
Gobiosoma sp.					*	*
Haemulon flavolineatum	*		*	*		
Haemulon plumieri	*	*				
Haemulon sciurus	*	*	*	*		
Halichoeres sp	*	*	*	*		
Hypoplectrus unicolor			*	*		
Lutjanus apodus	*		*	*		
Lutjanus griseus	*	*	*	*		
Lutjanus jocu			*			
Lutjanus mahogoni			*	*		
Ocyurus chrysurus			*	*		
Pseudupeneus maculatus				*		
Scarus sp	*	*	*	*		
Sparidae Type A					*	
Sparisoma sp	*	*	*	*		
Sphyraena barracuda			*	*		
Syngnathidae Type A					*	*

For all the life stages, this indicates that dissimilarity between the community structure of the two habitats arises mainly from the abundance of individual taxa, rather than their presence or absence. Individual taxa found across both habitats therefore show a preference for one habitat through differing abundances.

None of the assemblages show a significant difference between habitats when examined on the scale of Regions (ANOSIM: $R \leq 0.667$, $p \geq 0.100$). At the scale of Stations, however, the taxonomic composition of the night larval assemblage differs significantly between the mangroves and seagrass in Stations C and I (ANOSIM: $R = 0.079$, $p =$

0.012; R = 0.061, p = 0.040 respectively). In Station C, two thirds of the dissimilarity is due to 23 out of a possible total of 31 taxa (Table 7.3). Of these, 11 are found in both habitats. In Station I, the major proportion of the dissimilarity is due to 24 out of a possible total of 35 taxa, of which just 7 are present in both habitats. The difference between the mangrove and seagrass larval assemblages in both Stations appears to be mainly due to the presence or absence of taxa, although variation in the abundance of taxa found in both habitats is also a factor.

Both the juvenile and adult assemblages also show significant variation in taxonomic composition between habitats within Stations (Table 7.4). The juvenile assemblage varies significantly in Stations A to F, the adult assemblage in all Stations except E and H (ANOSIM: $R \geq 0.284$, $p \leq 0.040$). Approximately a third of the total taxa in each Station accounts for the differences between the mangrove and seagrass assemblages of juveniles and adults respectively. In contrast to the overall variation patterns, the difference between the mangrove and seagrass assemblages is due to the presence or absence of taxa, as well as their variation in abundance across the two habitats. Differences due to the presence or absence of taxa in turn arise largely from types present in the mangroves but absent in the seagrass.

Table 7.3. Night larval taxa accounting for approximately two thirds of dissimilarity between mangrove (M) and seagrass (S) assemblages of Stations C and I. Of these 11 out of 23 taxa in Station C and 7 out of 24 taxa in Station I are found in both habitats, indicating that the difference between the mangrove and seagrass larval assemblages in both Stations is due to the presence or absence of taxa, as well as the abundance of individual taxa.

	Station			
Taxa	**C**		**I**	
Atherinomorus stipes	M		M	S
Bathygobius curacao			M	S
Blennioidei Type A	M	S		
Blennioidei Type C			M	
Blennioidei Type D	M	S		S
Blennioidei Type E			M	S
Blennioidei Type F	M	S		
Blennioidei Type I				S
Blennioidei Type K		S		
Blennioidei Type M	M			
Brevoortia sp		S		S
Carapus bermudensis				S
Clupeidae Type A	M	S	M	
Ctenogobius saepepallens	M			
Doratonotus megalepis	M			
Engraulidae Type A				S
Eucinostomus lefroyi	M	S	M	
Gobiesox punctulatus	M	S		S
Gobiidae Type F			M	
Gobionellus sp			M	
Hypoplectrus sp	M	S	M	S
Jenkinsia parvula	M			
Malacoctenus sp			M	S
Microgobius gulosa		S		
Monacanthus sp	M	S	M	S
Parablennius marmoreus		S		
Pomacanthidae Type A	M	S		
Sardinella aurita	M	S		S
Scarus sp		S		
Sciaenidae Type A				S
Scorpaena sp				S
Sparisoma sp	M	S		
Sphoeroides maculatus	M			
Sphyraena barracuda			M	
Strongylura notata			M	
Syngnathidae Type A			M	S
Tripterygiidae Type A		S	M	

For the juveniles, 13 of the 14 taxa that account for the differences within the Stations also account for the overall variation between habitats, indicating relatively good agreement on the two scales. Similarly, for the adult assemblage, all 11 taxa that account for overall differences between the two habitats also account for variation within Stations. The same agreement is not apparent between the day

Table 7.4. Juvenile and adult taxa accounting for approximately two thirds of dissimilarity between mangrove (M) and seagrass (S) assemblages of Stations. Total number of taxa present in each Station are given in parentheses. Approximately a third of the total taxa in each Station accounts for the differences between the mangrove and seagrass assemblages, through either variation in abundance, or presence/absence.

Taxa	Station								
	A	B	C	D	E	F	G	H	I
Juveniles	*(28)*	*(25)*	*(20)*	*(21)*	*(22)*	*(20)*			
Abudefduf saxatilis			M						
Acanthurus sp		S	M	M	M				
Atherinomorus stipes					M				
Chaetodon capistratus	M								
Eucinostomus argenteus						M S			
Gerres cinereus		M S		M S	M S				
Haemulon flavolineatum	M S	M	M S	M S	M S	M S			
Haemulon sciurus		M S	M S	M S	M S	M S			
Halichoeres sp	S	S	M S						
Lutjanus apodus	M	M	M	M S	M	M			
Lutjanus griseus	M	M	M						
Lutjanus jocu				M		M			
Scarus sp	S	M S	M S	M S	M S	M S			
Sphyraena barracuda	M	M		M S	M S	M			
Adults	*(15)*	*(15)*	*(15)*	*(19)*		*(16)*	*(15)*		*(13)*
Abudefduf saxatilis				M					
Acanthurus sp									M
Atherinomorus stipes							M		
Eucinostomus argenteus				M S					
Gobiidae Type A	S		S			S			
Haemulon flavolineatum			M	M		M	M		M
Haemulon plumieri							M S		
Haemulon sciurus	M	M S	M S	M		M	M S		M
Halichoeres sp	S	M S	M S	M S		M S			
Lutjanus apodus		M		M			M		M
Lutjanus griseus	M	M S	M S	M S		M			M S
Ocyurus chrysurus							S		
Scarus sp	M S		M S	M		M S			M S
Sparisoma sp		M S	M S			M			

and night larval assemblages, however, which only show 5 taxa in common. While this reflects differences in habitat preference between the day and night larval assemblages, it also reflects the high number of contributing rare taxa.

Key points

Variation in assemblage composition is evident for each life-cycle stage of reef fish considered here. However, the manner and extent of variation differs between the respective life stages:

- the larval assemblages have a higher mean Shannon diversity index (H') value in the seagrass than in the mangroves, significantly so in the night assemblage;
- the mean H' values of the juvenile and adult assemblages are lower in the seagrass than in the mangroves;
- the proportion of species present as larvae, and therefore available to settle, is greater in the seagrass than in the mangroves;
- a larger proportion of taxa are recruited into the mangrove rather than the seagrass assemblages;
- H' values of juveniles show temporal variation in the seagrass, peaking in September;
- significant variation in assemblage composition between the mangrove and seagrass habitats is evident for the day larval, juvenile and adult assemblages, but not the night larval assemblage;
- dissimilarity in community structure arises mainly from the abundance of individual taxa, rather than their presence or absence;
- the night larval, juvenile and adult assemblages vary in composition between the two habitats on the scale of Stations nested within Regions, but not by Region.

7.2.2. Distribution of life-cycle stages of individual taxa across mangrove and seagrass habitats

The dissimilarities between the community structures of the two habitats arise mainly from the abundance of individual taxa, rather than their presence or absence. Therefore consideration of the relative abundance of individual taxa is necessary in order to establish whether settlement and recruitment are principally occurring in the mangrove or seagrass habitats. Twelve taxa are present in all three life stages, from which several trends of settlement and recruitment in the seagrass and mangrove habitats are apparent (Table 7.5).

Table 7.5. Relative abundance (%) of 12 taxa present as larvae, adults and juveniles in the mangroves (M) and seagrass (S). Although more adult taxa are present in the mangroves than the seagrass, the majority of larval taxa appear to settle in the seagrass. However, more taxa are recruited into the juvenile mangrove assemblage than the seagrass.

	Larvae		Juveniles		Adults	
Taxa	**M**	**S**	**M**	**S**	**M**	**S**
Atherinomorus stipes	17	83	100		100	
Chaetodon sp.	100		100		100	
Cryptotomus roseus		100	100		50	50
Eucinostomus jonesi	100			100	33	67
Halichoeres sp.	50	50	5	95	38	62
Hypoplectrus unicolor		100	11	89	33	67
Ocyurus chrysurus		100	7	93	8	92
Pomacentridae Type A		100	50	50	100	
Scarus sp.		100	26	74	50	50
Sparisoma sp.	13	87	12	88	40	60
Sphyraena barracuda	50	50	87	13	50	50
Strongylura notata	67	33	100			100

Only *Chaetodon* sp. appears to complete its life cycle in a single habitat, being present entirely in the mangroves as larva, juvenile and adult. Despite a high relative abundance of larvae in the seagrass, *Atherinomorus stipes* and *Cryptotomus roseus* appear to settle into the mangrove habitat, where they are found entirely as juveniles. However, this indicates that the seagrass larval assemblage is supplying the mangrove population. While adult *A.stipes* remain in the mangroves, *C.roseus* are distributed evenly between the two habitats, indicating migration from the mangroves to the seagrass on reaching adulthood.

Eucinostomus jonesi larvae are present only in the mangroves, and yet recruitment to the juvenile assemblage occurs only in the seagrass. However, adults are present in the mangroves as well as the seagrass, suggesting that spawning occurs in the mangrove habitat, with recruitment and development to adulthood taking place in the seagrass beds. The same may apply to *Halichoeres* sp., which although evenly distributed between the two habitats during its larval stage shows a relatively high recruitment to the seagrass. At the adult stage there is a movement back to the mangrove habitat, although a greater proportion is present in the seagrass beds. A more distinct pattern is evident for *Hypoplectrus unicolor*, *Ocyurus chrysurus*, *Scarus* sp. and *Sparisoma* sp., with the majority of settlement, recruitment and adult development occurring in the seagrass beds.

Another pattern is shown again by the relative abundance of Pomacentridae Type A. The lack of larvae in the mangroves indicates that settlement occurs into the seagrass. The even distribution of juveniles across the two habitats indicates that migration to the mangroves then takes place. This is supported by the lack of adults in the seagrass, which also indicates that adult development is completed in the mangroves.

The final two species, *Sphyraena barracuda* and *Strongylura notata*, both have a relatively even distribution as larvae between the two habitats, but the high relative abundance of juveniles indicates they settle mainly in the mangroves. However, adult *S.barracuda* show an even distribution again between the two habitats, while adult *S.notata* are only evident in the seagrass beds.

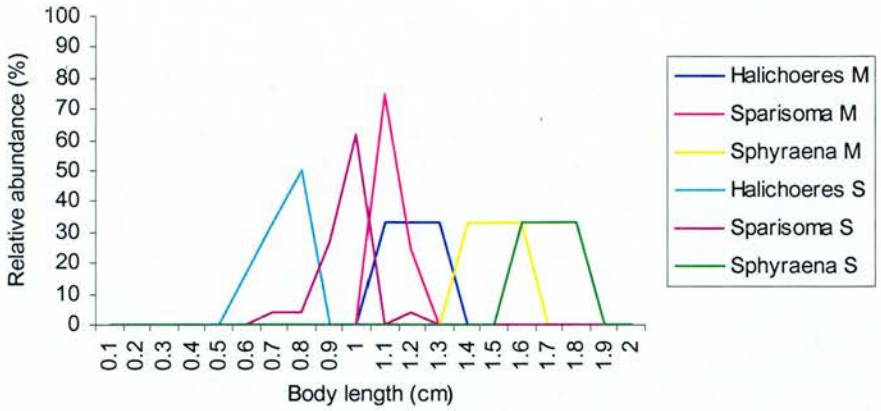
Distribution processes may be clarified by further consideration of *Halichoeres* sp., *Sparisoma* sp. and *Sphyraena barracuda*, for which all three developmental stages are present across both habitats.

Table 7.6. Mean total body length (cm) ± standard error of three taxa present as larval, juvenile and adult stages across both mangrove (M) and seagrass (S) habitats. * denotes significant variation between mangrove and seagrass means of the respective life stage.

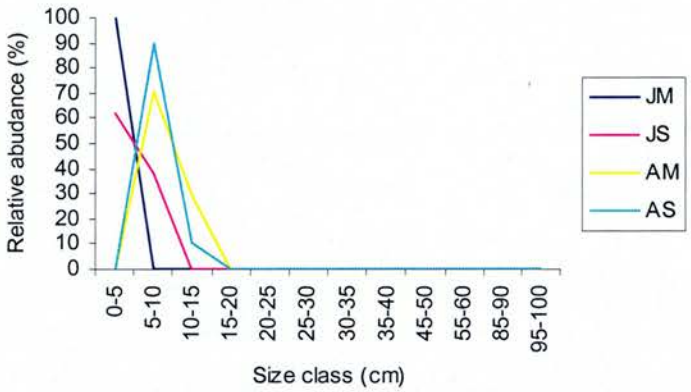
	Larvae		Juveniles		Adults	
	M	S	M	S	M	S
Halichoeres sp.	1.20* (0.06)	0.70 (0.06)	4.71 (0.29)	5.52 (0.11)	11.46* (0.36)	10.34 (0.16)
Sparisoma sp.	1.11* (0.03)	0.96 (0.02)	10.00* (0.90)	6.53 (0.40)	17.61 (1.37)	15.86 (0.38)
Sphyraena barracuda	1.50 (0.06)	1.70 (0.06)	21.00* (1.10)	35.2 (3.20)	52.00 (2.00)	74.00 (8.72)

Although the larvae of *Halichoeres* sp. are evenly distributed among the mangrove prop-roots and seagrass beds, its biomass differs between the habitats (Figure 7.2). The mean body length of *Halichoeres* sp. is significantly greater in the mangroves than in the seagrass, indicating that smaller and therefore younger larvae are present in the seagrass beds than in the mangroves. This suggests in turn that larval supply originates in or over the seagrass, with subsequent movement to the mangroves apparent. The juvenile stage shows no significant difference in biomass between the habitats, with a slightly higher mean in the seagrass. The relative abundance shows a marked difference, however, with 95 % of juveniles in the seagrass, indicating that settlement largely occurs there. At the adult stage, the mean body length in the mangroves is again significantly greater than in the seagrass, while the relative abundance remains lower in the mangroves at 38 % than in the seagrass at 62 %. This indicates a movement to the mangrove habitat by larger and therefore older individuals.

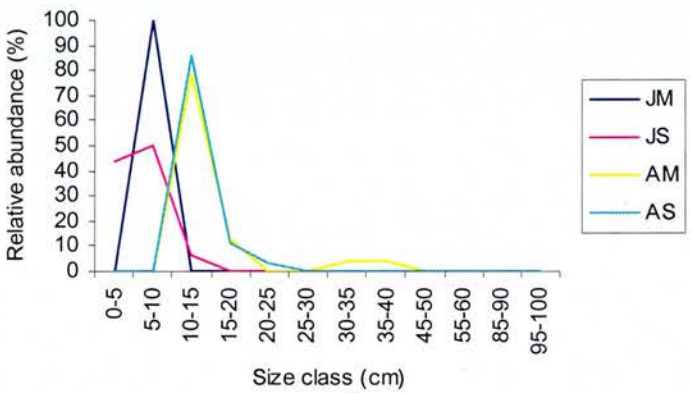
The mean larval body length of *Sparisoma* sp. is also significantly greater in the mangroves than in the seagrass, indicating that smaller, younger larvae predominate in the seagrass beds than in the mangroves. The relative larval abundance is much higher in the seagrass at 87 %,



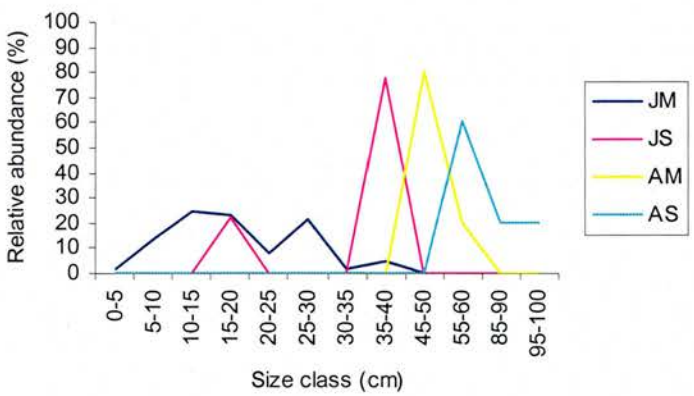
(a)



(b)



(c)



(d)

Figure 7.2. Relative abundance of *Halichoeres* sp., *Sparisoma* sp. and *Sphyraena barracuda* larval body length (a), and juvenile (J) and adult (A) size classes (a-c) in the mangrove (M) and seagrass (S) habitats. The larval body length and juvenile size class distributions of all three taxa show distinct separation between the two habitats, whereas the adult size class distributions overlap.

suggesting in turn that larvae are originating in or over the seagrass, with some movement to the mangroves by older individuals. A similar distribution in abundance for the juvenile stage, with a significantly lower mean body length in the seagrass, indicates that settlement largely occurs into the seagrass beds. A more even distribution is apparent at the adult stage, with no significant difference in mean body length between the habitats. This indicates movement to the mangrove habitat by larger, older individuals, for example as part of diurnal migration patterns, or ontogenetic migration.

Larval *Sphyraena barracuda* show an even distribution between the two habitats, with no significant difference in mean body length, although it is higher in the seagrass. This suggests larval supply originates in the mangroves, in a contrasting pattern to the previous two taxa. The juvenile distribution also contrasts, with 87 % in the mangroves, and the mean body length, which is significantly lower in the mangroves than in the seagrass beds. Settlement therefore is predominantly in the mangrove habitat. An even distribution is apparent again at the adult stage, with larger fish in the seagrass than in the mangroves, although the difference in size is not significant. This movement to the seagrass habitat by larger, older individuals indicates diurnal migration patterns, or ontogenetic migration.

Key points

For the 12 taxa present in all three life-cycle stages, the contrasting patterns of distribution between the seagrass and mangrove habitats at different stages may be summarised:

- only *Chaetodon* sp. remains in a single habitat, the mangroves, throughout its life-cycle;
- *Atherinomorus stipes*, *Cryptotomus roseus*, *Sphyraena barracuda* and *Strongylura notata* appear to settle predominantly in the mangroves, although adults and/or larvae are predominantly found in the seagrass;

- *Eucinostomus jonesi*, *Halichoeres* sp., *Hypoplectrus unicolor*, *Ocyurus chrysurus*, Pomacentridae Type A, *Scarus* sp., and *Sparisoma* sp. predominantly settle in the seagrass, although adults and/or larvae are found in the mangroves;
- for *Halichoeres* sp., the mean larval and adult body length is significantly greater in the mangroves than the seagrass;
- for *Sparisoma* sp. the mean larval and juvenile body length is significantly greater in the mangroves than the seagrass;
- for *S.barracuda* the mean juvenile body length is significantly lower in the mangroves than in the seagrass;
- migration from the seagrass to the mangroves is apparent for *Halichoeres* sp. and *Sparisoma* sp., and from the mangroves to the seagrass for *S.barracuda*.

7.2.3. Variation of environmental variables and fish assemblages between habitats

Variation in the taxonomic composition of the larval, juvenile and adult assemblages between the two habitats appears to be influenced by several environmental variables (Table 7.7). However, BIO-ENV analysis, in which the relevant matrix of environmental variables is correlated with the larval, juvenile or adult assemblage, shows that a wide range of abiotic variables may be linked to the composition of the respective assemblages, and potential causal relationships are difficult to pinpoint as a result.

Spatial variation of day and night larval assemblages

Variation evident in individual environmental factors between the mangrove and seagrass habitats provides an initial indication of how the two habitats vary. The mean extinction coefficient calculated for the mangroves is significantly higher than that for the seagrass beds, whereas the mean wind velocity, water depth, nitrate ion concentration and salinity values calculated are significantly higher in the seagrass than the mangroves (Two sample T-tests: $T \leq 3.19$, $p \leq 0.028$).

Table 7.7. Summary of BIO-ENV analysis of spatial variation in environmental factors against larval, juvenile and adult assemblages in the mangrove and seagrass habitats. * indicates variables that maximise the matching Spearman rank correlation coefficient between the environmental matrix, and the corresponding assemblage matrix at species and family level. † indicates variables with significantly higher mean than in unmarked habitat ($p < 0.05$). Larval assemblages collected at night by light trap and during the day by plankton net tow are analysed separately. In the mangroves, neither the extinction coefficient nor the turbidity maximise the coefficient. In the seagrass, all the variables maximise one or more coefficients. This indicates that in the mangroves, the extinction coefficient and turbidity are of weaker influence in determining the assemblage compositions than the other environmental variables, whereas in the seagrass all the variables are influential for at least one assemblage type.

	Night larva		Day larva		Juvenile		Adult	
	Species	Family	Species	Family	Species	Family	Species	Family
Environmental variable								
Mangrove								
Water temperature (°C)	*	*	*	*	*		*	*
†Extinction coefficient								
Wind velocity (m/s)	*		*					
Water depth (m)					*	*	*	*
Turbidity (FTU)								
Sulphate (mg/l)	*	*						
Nitrate (mg/l)		*			*	*	*	*
Salinity (‰)				*				
pH			*					
Correlation coefficient	**0.361**	**0.471**	**0.294**	**0.213**	**0.757**	**0.692**	**0.665**	**0.604**
Seagrass								
Water temperature (°C)				*	*			*
Extinction coefficient	*	*						*
†Wind velocity (m/s)			*	*			*	*
†Water depth (m)	*	*	*	*	*	*	*	*
Turbidity (FTU)		*						
Sulphate (mg/l)		*			*			
†Nitrate (mg/l)	*	*		*	*	*		
†Salinity (‰)		*						
pH	*							
Correlation coefficient	**0.705**	**0.684**	**0.550**	**0.725**	**0.544**	**0.443**	**0.383**	**0.257**

Both the night and day larval assemblages show higher correlation with the environmental variables in the seagrass beds than the mangrove prop-roots, indicating that the influence of the abiotic variables is greater in the former than the latter. For the mangrove night larval population, water temperature and sulphate ion concentration both maximise the matching coefficient, along with wind velocity and nitrate ion concentration at species and family level respectively (Table 7.7). Wind velocity and nitrate ion concentration are both significantly lower in the mangrove habitat than in the seagrass, suggesting that low wind (i.e. good shelter from wind) and nitrate (i.e. low input from seagrass) influence the larval assemblage at night.

The extinction coefficient, water depth and nitrate ion concentration maximise correlation with the night larval supply, along with pH at species level, and salinity, turbidity and sulphate ion concentration at family level. As nitrate also influences the mangrove larval assemblage, its variation between the two habitats may well have an effect on assemblage composition. In addition, salinity and water depth are significantly higher in the seagrass than the mangroves, and the extinction coefficient is significantly lower, all of which may be influencing the larval assemblage composition.

For the day larval mangrove population, water temperature again maximises correlation, along with wind velocity and pH at the species level, and salinity at the family level. Wind velocity and water depth both maximise correlation with the seagrass day larval assemblage, in addition to water temperature and nitrate ion concentration at the family level. As wind velocity, water depth and nitrate ion concentration are all significantly greater in the seagrass, their variation between the two habitats may be influential in determining the larval assemblage composition. No single environmental variable is influential across both habitats, at both taxonomic levels, of both the day and night larval assemblages.

In contrast to the larvae, the rank correlation between the juvenile assemblage and the abiotic data matrix is relatively high in the mangrove habitat compared to the seagrass. At species level the coefficient for the mangrove juvenile assemblage is maximised by water temperature, depth and nitrate ion concentration. In the seagrass, water temperature, depth, sulphate and nitrate ion concentration maximise correlation at the species level. At the family level only water depth and nitrate ion concentration are required for both habitats. Both vary significantly between habitats and also influence the assemblages of both habitats at the species level, indicating a relatively strong link between them and the juvenile assemblage composition.

The adult assemblages also have a much lower correlation with the seagrass environmental variables than those of the mangroves. The coefficient for the mangrove adult assemblage data at both species and family level, is maximised by water temperature, depth and nitrate ion concentration. For the seagrass adult assemblage data, only wind velocity and water depth maximise correlation at the species level, while at the family level the extinction coefficient and water temperature are also required. Variation in the adult assemblage between the two habitats may therefore be influenced by the significantly higher water depth, nitrate ion concentration and wind velocity, and lower extinction coefficient, in the seagrass.

Temporal variation of day larval assemblages

Habitat and date are both significant factors in determining the species and family composition of the day larval assemblages (2-way crossed ANOSIM: $R \geq 0.116$, $p \leq 0.001$). As the majority of the environmental factors measured vary with time, they may also influence the temporal variation of the larval assemblages (Appendix 4.1). Significant temporal variation is apparent in the levels of the environmental variables with sampling date in both the mangrove and seagrass

habitats (ANOSIM: R = 0.486, $p \leq 0.001$; R = 0.498, $p \leq 0.001$ respectively).

For the mangrove larval population and the linked abiotic data, only nitrate ion concentration is required to maximise the matching coefficient, at both taxonomic levels (Table 7.8). As all the variables differ significantly with date, variation in nitrate may be influential.

Table 7.8. Summary of BIO-ENV analysis of environmental variables and day plankton net tow assemblages, by sampling date. * indicates variables that maximise the matching Spearman rank correlation coefficient between the environment matrix, and the larval population and supply matrices at species and family level. All show significant variation with date ($p < 0.05$).

	Larval population		**Larval supply**	
	Species	Family	Species	Family
Environmental variable				
Water temperature (°C)				
Extinction coefficient			*	
Wind velocity (m/s)				
Water depth (m)				
Turbidity (FTU)			*	
Sulphate (mg/l)			*	*
Nitrate (mg/l)	*	*		*
Salinity (‰)				
pH			*	*
Correlation coefficient	**0.175**	**0.337**	**0.448**	**0.406**

However, the relatively low correlation values with the mangrove larval population indicate that these abiotic factors have little influence on the temporal variation of the day larval assemblage composition. A stronger influence of environmental variables is apparent in the seagrass habitat, which in turn is more exposed and therefore more vulnerable to temporal changes in abiotic variables. Sulphate ion concentration and pH both maximise the correlation, along with the extinction coefficient and turbidity at the species level, and nitrate ion concentration at the family level. Although a direct causal relationship cannot be assumed, all may be influential.

Key points

The influence of the environmental variables on the composition of the larval, juvenile and adult assemblages can be summarised as:

- the larval assemblages show a stronger correlation with environmental variables in the seagrass habitat, while the juvenile and adult assemblages show a stronger correlation in the mangroves;
- the mean extinction coefficient is significantly greater in the mangroves than in the seagrass, while the mean values of wind velocity, water depth, nitrate ion concentration and salinity are significantly greater in the seagrass than the mangroves;
- all the environmental variables maximise the correlation coefficients between the assemblages and the environmental matrices;
- all the environmental variables show significant variation with date, and although correlation with the day mangrove larval population is low, it is relatively high with the seagrass assemblage.

7.3. *Discussion*

The larval assemblage of both habitats is dominated by similar taxa, namely *Hypoplectrus* sp. and *Atherinomorus stipes*, as well as several types of blennioids, cluepeids, gerreids, gobiids, pomacanthids and syngnathids. The mean Shannon Diversity Index value is significantly higher in the seagrass than in the mangroves, indicating a greater number of rare species in the former habitat. Shulman (1984) and Dennis (1992) both suggest the fine structure of the seagrass habitat makes it a more suitable refuge for early larval stages, and indeed the mean larval size recorded here is significantly smaller in the seagrass than in the mangroves.

Although the *Hypoplectrus* larvae collected were too young to be identified to species level, their small size (< 0.5 cm) indicates that

spawning occurred very close to or in the mangroves and adjoining seagrass beds. The genus is generally reef-associated and has been reported from the outer reef habitat of Turneffe Atoll previously (Domeier & Colin, 1997; Harbourne, 2000), but the presence of juveniles and adults in the mangrove and seagrass habitats indicates settlement and recruitment to a local population is occurring within the atoll lagoon.

Atherinomorus stipes has not been reported from the outer reef habitat of the atoll, although it has a wide habitat range, which includes coral reef (Cervigón *et al.*, 1992; Lieske & Myers, 1994; Harbourne, 2000). As a small shoaling fish, it often dominates assemblages in high densities and is often excluded from analyses as a result, making comparisons with other studies difficult (Thayer *et al.*, 1987; Boulon, 1992; Dennis, 1992; Sponaugle & Cowen, 1996; Ley *et al.*, 1999; Claro & Parenti, 2001). Although adults and juveniles are also predominant in the mangroves of Calabash Cay, only larvae are present in the seagrass, indicating that spawning and settlement occur in the mangroves. Thayer *et al.* (1987) also reported *A.stipes* adults solely from mangroves during a survey of mangrove and adjoining seagrass habitats.

The suborder Blennioidei comprises six families: Blenniidae, Chaenopsidae, Clinidae, Dactyloscopidae, Labrisomidae, and Tripterygiidae (Springer and Freihofer, 1976; George and Springer, 1980; Springer, 1993). They primarily inhabit coral reefs, although some families, such as Dactyloscopidae and Blenniidae, are found brackish environments (Springer and Gomon, 1975; Matarese *et al.*, 1984; Nelson, 1994). Together with Syngnathidae and Gobiidae, Blennioidei are typically cryptic and the apparent absence of their juvenile and adult stages in the results of the visual census surveys is therefore not surprising. Although all 3 groups are reported from the outer reef, gobies and blennies are both benthic rather than pelagic

spawners, and syngnathids are livebearers generally associated with vegetated shallow-water habitats, implying that the larvae are produced by local populations (Richards & Lindeman, 1987). However, this does not preclude movement between habitats to breed, as shown by goby species recorded moving into mangroves to breed (Ogden & Gladfelter, 1983).

Another common larval family, the clupeids are coastal schooling fishes, with many species found in brackish water and some associated with beds of the seagrass genus *Thalassia* (Whitehead, 1985). Although no juveniles or adults were recorded in visual census surveys, large shoals were observed in both habitats (Cavers, pers.obs.). They are typically nocturnal, with diurnal resting schools seasonally shifting location between coastal habitats (Ogden & Gladfelter, 1983; Valdés-Muñoz & Mochek, 2001)

Gerreids are also associated with brackish water, in particular mangrove areas and vegetated sand grounds (Cervigón *et al.*, 1992; Dennis, 1992; Greenfield & Thomerson, 1997). Together with the recorded presence of juveniles and adults of *Eucinostomus argenteus*, *Eucinostomus jonesi* and *Gerres cinereus*, this suggests local populations complete their full life cycle in the mangroves and seagrass beds. The most abundant gerreid larva, *Eucinostomus lefroyi*, was recorded in both habitats, but was absent as juveniles or adults. However, previous studies recorded adult *E.lefroyi* from the outer reef (Harbourne, 2000). As it is generally a reef-associated species and a pelagic spawner, the seagrass and mangrove larval populations are most likely the offspring of adult populations from the outer reef. The family Pomacanthidae is also generally associated with shallow water (< 20 m) coral reefs and consists of pelagic spawners. The presence of adults and juveniles in the mangroves implies larvae are produced by transient local populations, with migration to the coral reef probably occurring once development to adulthood is complete.

There is a marked decrease in species richness from 50 juvenile taxa to 36 adult types. As with larvae, juveniles are lost through migration between habitats and natural mortality. Although predation and disease are both major sources of natural mortality in juvenile fishes, most mortality can be explained by predation rather than disease (Carr & Hixon, 1995; Connell, 2000). Migration during the juvenile stage of coral reef fish has been frequently recorded, in particular for the Haemulidae and Lutjanidae (Ogden & Ehrlich, 1977; Valdés-Muñoz & Mochek, 2001). Haemulids, lutjanids and scarids are predominant in the juvenile and adult assemblages, alongside *Atherinomorus stipes*.

The juvenile mangrove assemblage of Calabash is dominated by *Haemulon flavolineatum*, a common inhabitant of the mangrove ecosystem (Dennis, 1992; Claro & García-Arteaga, 1993; Sedberry & Carter, 1993). Few haemulid larvae were retrieved from light-traps in the present study, and none from the plankton-net tows, which is surprising as many species are considered continuous spawners, with juveniles observed throughout the year (Munro *et al.*, 1973; Lindeman, 1986; García-Cagide *et al.*, 2001). However, haemulid larvae are generally not well represented in light-traps (Watson, pers.comm.). Also, haemulids are thought to form offshore spawning aggregations (García-Cagide *et al.*, 2001; Lindeman *et al.*, 2001), in which case larvae may not be apparent in shallow coastal habitats until close to settlement. As adult *H.flavolineatum* have been recorded previously as abundant on the outer reef (Harbourne, 2000), it is proposed that spawning occurs offshore, larvae are transported inshore and settle into the mangroves, migrating to seagrass beds as juveniles and adults, and eventually returning to the outer reef.

The diel migration of Haemulidae between habitats offering shelter to more open feeding-grounds, is well documented (Randall, 1967; Starck, 1971; Helfman *et al.*, 1982; Parrish, 1989; Nagelkerken *et al.*,

2000a; Valdés-Muñoz & Mochek, 2001). On Calabash the relative abundance of adult *H.flavolineatum* is very similar in the two habitats, implying that the more vulnerable juveniles need to seek shelter in the mangroves during the day, while the adult population, larger and less at risk, move further afield. In contrast, *Haemulon sciurus* has a relatively high abundance in the seagrass as a juvenile, and a very high abundance in the mangroves as an adult. A similar pattern for *H.sciurus* was observed by Sedberry & Carter (1993), who suggested juveniles were migrating towards the reef from the mangroves, while adults were foraging away from their coral reef residences. The differences observed on Calabash in the juvenile distributions of the two species may reflect seasonal variation in settlement and recruitment, with an older assemblage of *H.sciurus* juveniles migrating via the seagrass beds to the outer reef habitat while a younger assemblage of *H.flavolineatum* settles into the mangroves. However, behavioural differences in these two species are reported by Valdés-Muñoz & Mochek (2001), who recorded frequent use of shelters by *H.flavolineatum* and limited use of shelters by *H.sciurus*.

Adult and juvenile distribution patterns are often related, and the distribution of juvenile haemulids has been shown to correlate inversely with adult distributions, probably as a result of differing habitat and food preferences (Lindeman, 1986; Tupper & Juanes, 1999). In addition, late stage juvenile haemulids have been recorded recruiting to mangrove habitats (Ley *et al.*, 1999). Therefore it is proposed that *H.sciurus* spends most of its juvenile stage in the seagrass, moving to the mangroves late on to complete its transition to adulthood, before migrating to the outer reef.

Juvenile and adult *Lutjanus apodus* and *Lutjanus griseus* have a relatively high abundance in the mangrove habitat compared to the seagrass. *L.griseus* is also referred to as the mangrove snapper due to its affinity with the mangrove habitat at all life-stages, and *L.apodus* is

often associated with it (Starck, 1971; Manooch & Matheson, 1983). As with the haemulids, spawning tends to occur offshore, with larvae commonly reported from offshore rather than inshore areas (Starck, 1971; Leis, 1987; Richards & Lindeman, 1987). However, spawning strategies vary, with continental snapper populations generally showing seasonal peaks in production while island populations tend to spawn continuously (Grimes, 1987).

Approximately 50 % of the taxa recorded do appear to have an obligate dependency on either the mangroves or the seagrass at one or more of their life stages. However, as many constitute less than 1 % of the respective larval, juvenile or adult assemblage of either habitat, their definition as obligate mangrove or seagrass residents cannot be treated as steadfast. Of the 8 taxa present at all three life stages, none were confined to a single habitat. Little difference in general food type availability is apparent between the mangroves and seagrass, and the main difference between the habitats is their structure, reflecting in turn the amount of shelter available for and from predators. Shelter and predation pressure are therefore proposed as more influential in determining species distribution than food availability. Some indication of this is gained by consideration of *Halichoeres* sp., *Sparisoma* sp. and *Sphyraena barracuda*, which have marked differences in ecology and are present across both habitats in all three life stages.

Both diurnal, the labrid *Halichoeres* sp. and scarid *Sparisoma* sp. are characteristic of coral reefs and seagrass beds, and often observed together in mixed shoals, although the former is a generalised carnivore and the latter a herbivore (Randall, 1967; Valdés-Muñoz & Mochek, 2001). The herbivores and generalised carnivores constitute the two feeding guilds with the greatest relative abundance in both habitats. The soft-bottomed mangrove habitat and seagrass beds have a high density of benthic invertebrates for general carnivores, while

algae on mangrove prop-roots and the seagrass plants provide an extensive food source for herbivores. Another scarid genus, *Scarus* sp., constitutes the most abundant juvenile and adult in the seagrass habitat of Calabash, and is therefore worth considering with *Sparisoma* sp. due to their similar ecology.

Scaridae are generally reported migrating from nocturnal refuges in coral reefs to grazing grounds in seagrass beds (Parrish, 1989; Sedberry & Carter, 1993; Valdés-Muñoz & Mochek, 2001), but the presence of larval, juvenile and adult stages in the mangroves of Calabash indicates that prop-roots also serve as a refuge. *Scarus guacamaia* is reported to have an obligate juvenile dependency on mangroves, principally as a shelter (Dennis, 1992; Mumby *et al.*, in press), although it has also been reported from seagrass (Randall, 1967; Overholtzer & Motta, 1999). Scarids as well as haemulids are recorded prey of *Lutjanus* spp. (Randall, 1967; Starck, 1971), and therefore a preference for areas with a high availability of shelter is expected. A significant presence of diurnal predators in seagrass beds, such as the young juvenile stage of *Lutjanus griseus*, may confine scarids to the shelter of mangrove stands where available. The reverse is apparent in the present study, however, with a high relative abundance of juvenile *Lutjanus* spp. in the mangroves and a very low one in the adjacent seagrass beds.

Sphyraena barracuda is a diurnal predator, in particular of fishes, and is an established resident of mangrove and seagrass habitats in its larval and juvenile stages (De Sylva, 1963; Randall, 1967; Schmidt, 1989; Dennis, 1992; Claro & Parenti, 2001). As a top carnivore it is generally solitary even as a juvenile. Some researchers suggest this also results in low larval abundances, and have used this to explain low catches of *Lutjanus* spp. larvae.

However, the larval stages of many carnivores including the Lutjanidae are initially planktivorous. The complex structure of the mangrove and seagrass habitats, combined with shallow water, acts as an effective trap for zooplankton. For adult zooplanktivores, however, the restricted environment limits feeding efficiency, resulting in a relatively low abundance. Not only do these complex habitats trap a potential food source for fish larvae, they also act as a sink for the larvae themselves.

In terms of overall taxonomic composition, the larval, juvenile and adult reef fish assemblages differ significantly when compared by month, implying high levels of ontogenetic migration to and from the mangrove and seagrass habitats. Variation in assemblage composition is also evident between the seagrass and mangrove habitats for each life-cycle stage, although the extent of variation differs between the respective life stages. The larval assemblages have a higher mean Shannon diversity index value in the seagrass than in the mangroves, significantly so in the night assemblage, suggesting a higher diversity of larval supply to the mangroves than the eventual resident larval population. By contrast the mean diversity values of the juvenile and adult assemblages are lower in the seagrass than in the mangroves. Although the proportion of species present as larvae, and therefore available to settle, is greater in the seagrass than in the mangroves, a larger proportion of taxa settles in the mangroves. Therefore if settlement is occurring in the seagrass, it is closely followed by migration to the mangrove habitat. This implies recruitment to the mangroves is higher, but it could also be a reflection of diel migration patterns, due to the proximity of the two habitats.

The larval assemblage in the mangroves appears to be partly influenced by the environmental variables measured. All the environmental variables exhibit significant spatial and temporal variation, and show high levels of correlation with the day seagrass larval assemblage but

not the mangrove population. It is not surprising that significant temporal variation is evident, as sampling was undertaken from June, during which weather conditions are relatively stable, to November, which is in the hurricane season and associated with unsettled weather conditions. The more sheltered aspect of the mangrove habitat could limit circulation and therefore seasonal changes in environmental variable parameters. In the seagrass, larval taxonomic composition is correlated with sulphate and nitrate ion concentrations, pH, the extinction coefficient and turbidity. Increased levels of the latter two factors lead to decreased risk of photodamage and visual predation. However, the influence of environmental variables on reef fish distribution requires further experimental investigation, as studies disagree on the importance of abiotic factors (Blaber & Blaber, 1980; Bell *et al.*, 1984).

Only the juvenile seagrass assemblage shows a significant temporal variation in mean diversity values, with a peak in September. A significant variation in assemblage composition between the mangrove and seagrass habitats is evident for the day larval, juvenile and adult assemblages, but not the night larval assemblage. This could be heavily influenced by the decreased larval stratification evident at night. Dissimilarity in community structure between the mangroves and seagrass assemblages arises mainly from the abundance of individual taxa rather than their presence or absence, as most are common to both habitats. This indicates migration between the two habitats. The night larval, juvenile and adult assemblages vary in composition between the two habitats on the scale of Stations nested within Regions, but not by Region.

Twelve taxa are present in all three life-cycle stages, and show contrasting patterns of distribution between the seagrass and mangrove habitats at different stages. Only *Chaetodon* sp. remains in a single habitat, the mangroves, throughout its life cycle. *Atherinomorus stipes*,

Cryptotomus roseus, *Sphyraena barracuda* and *Strongylura notata* appear to settle predominantly in the mangroves, although adults and/or larvae are predominantly found in the seagrass. *Eucinostomus jonesi*, *Halichoeres* sp., *Hypoplectrus unicolor*, *Ocyurus chrysurus*, Pomacentridae Type A, *Scarus* sp., and *Sparisoma* sp. predominantly settle in the seagrass, with the adult and/or larval stages mainly found in the mangroves.

Although *Halichoeres* sp. is present in both the mangrove and seagrass habitats during each stage of its life cycle, its mean larval and adult body length is significantly greater in the mangroves than the seagrass. These mangrove individuals are less vulnerable to predation than their younger seagrass counterparts. The same is true of *Sparisoma* sp. larvae and juveniles, also present in both habitats. The mean juvenile body length for *Sphyraena barracuda* is significantly lower in the mangroves than in the seagrass. The size-distribution of the juvenile stages of *Halichoeres* sp., *Sparisoma* sp. and *S.barracuda* indicate the former two migrate from the seagrass to the mangroves, while the latter moves from the mangroves to the seagrass beds. The movement of *S.barracuda* could be a reflection of its open water feeding technique, as more space is available in the open water over the seagrass than in the complex structure of the mangroves. In turn, while *Halichoeres* sp. and *Sparisoma* sp. are less vulnerable to predation with increasing size, they may have outgrown the shelter available in the seagrass habitat, and may also be avoiding immigrating diurnal predators such as *S.barracuda*.

8.0 Differential habitat use by larval, juvenile and adult reef fish in the mangroves

8.1. *Introduction*

Predation and starvation are regarded as two of the most important factors for the survival of marine fauna, and are generally used to explain the nursery role of mangroves (Lasker, 1987; Baran & Hambrey, 1998). The high productivity of mangroves allows the development of a dense zooplanktonic and benthic fauna, a plentiful food source for the mainly planktivorous larval, juvenile and adult fish assemblages present in the mangroves (Houde & Shekter, 1993; Whitfield, 1999). Fish are in turn at risk of predation, from carnivorous holoplankton such as copepods and adult planktivores such as Gobiidae during their larval stage, or each other during all three stages (Hunter, 1981; Brewer *et al.*, 1995; Dittel *et al.*, 1997).

Many authors indicate that reduction of predation efficiency in nursery habitats is related to the structural complexity of the habitat, or turbidity of the water (Robertson & Blaber, 1992). The dense web of mangrove prop roots provides extensive shelter for late stage larvae and juveniles from large and small predators (Robertson & Duke, 1987; Thayer *et al.*, 1987; Al-Khayat and Jones, 1999). Overshadowing and increased turbidity also limit predator visibility, lessening the need for diel vertical migration, a behavioural strategy used to avoid predation by which planktonic and nektonic organisms rise to the surface to feed at dusk, and sink again at dawn (Helfman, 1981; Laroche *et al.*, 1997; Abello & Guerao, 1999). Reverse diel migrations are evident in planktivores and piscivores, which remain at or near the water surface throughout the diel cycle (Ryer & Olla, 1999). To test these ideas the following research question is posed: Is prey availability a more significant factor than shelter availability in habitat selection by reef fish, especially juveniles?

8.2. *Results*

8.2.1. Variation of larval, juvenile and adult life stages within the mangrove habitat

Variation in assemblage composition of the night larval population appears low when analysed by area, with all Regions grouped together at a Bray-Curtis similarity level of 55 % (Figure 8.1). The entire day larval population is grouped at 40 % similarity. A higher level of similarity is evident between the juvenile and adult assemblage composition of each Region, with all Regions grouped at 75 % similarity.

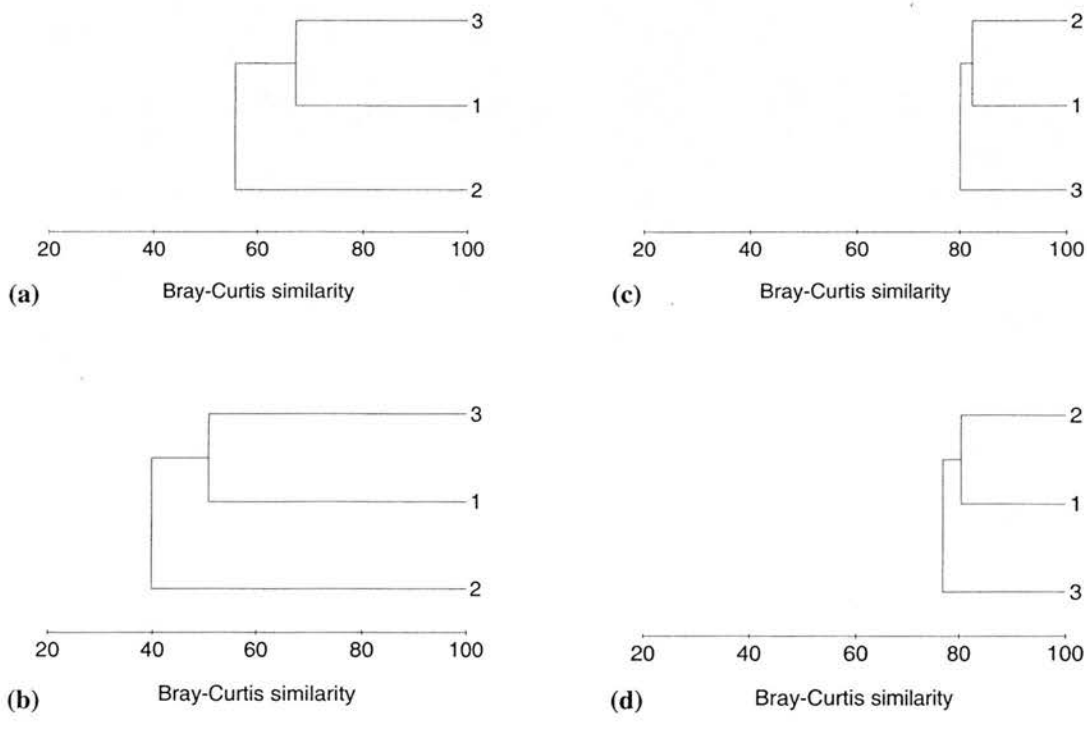


Figure 8.1. Dendrograms for hierarchical clustering (group-average linking) of Regions 1, 2 and 3 based on family composition of (a) night larval, (b) day larval, (c) juvenile and (d) adult assemblages from the mangrove habitat. A high level of Bray-Curtis similarity is evident for all, ranging from 40 % for the day larval assemblage to 80 % for the juvenile mangrove assemblage.

The night and day larval population assemblages both differ significantly between Regions (ANOSIM: $R \geq 0.342$, $p \leq 0.014$). The

transects covered by a single plankton net tow encompass all three Stations in a single Region, and therefore larval data can only be broken down to a Regional level. For the day larvae, a total of 17 taxa out of a possible 22 account for approximately two thirds of the dissimilarity between the Regions (Table 8.1). No taxa are present across all 3 Regions, indicating that the presence or absence of taxa, rather than varying abundances, accounts for the major proportion of dissimilarity between the groups.

Table 8.1. Larval population taxa collected by plankton net accounting for approximately two thirds of dissimilarity between Regions, based on CLUSTER analysis at 50 % Bray-Curtis similarity. Presence is denoted by *. No taxa are present across all 3 Regions, indicating that presence/absence of taxa rather than abundance accounts for most dissimilarity between the groups.

Taxa	Region Groups		
	1	2	3
Achirus lineatus		*	
Bathygobius sp.			*
Brevoortia sp.	*		*
Eleotris sp.	*	*	
Eucinostomus lefroyi			*
Gobiesox punctulatus			*
Gobiosoma sp.	*		*
Jenkinsia lamprotaenia		*	
Lycengraulis grossidens			*
Micrognathus sp.	*		
Monacanthus setifer			*
Monacanthus sp.	*	*	
Pomacanthidae Type A			*
Scorpaena sp.			*
Sparidae Type A	*		
Strongylura notata			*
Syngnathidae Type A	*		

The night larval assemblage can be analysed on the level of Stations, however, and also differs significantly between Stations nested within Regions (ANOSIM: R = 0.030, p = 0.036). According to a SIMPER routine, 45 taxa out of a possible total of 73 account for approximately two thirds of the dissimilarity between the groups of Stations clustered according to their night larval population assemblages (Table 8.2). As no single species is present across all the groups, the presence or absence of taxa rather than their abundance is assumed to be principally responsible for the clustering of Stations.

Table 8.2. Larval population taxa collected by light trap accounting for approximately two thirds of dissimilarity between groups of Stations, based on CLUSTER analysis at 50 % Bray-Curtis similarity. Presence is denoted by *. Groups 1 and 2 encompass Stations A, B, C and D, E, F respectively, 3 encompasses Stations G and H, and 4 is Station I.

Taxa	Station Groups			
	1	2	3	4
Acanthemblemaria chaplini	*			
Anchoa lamprotaenia	*			
Anchoviella perfasciata		*		
Astrapogon sp				*
Atherinomorus stipes	*	*		
Bathygobius curacao	*	*		
Blennioidei Type A	*	*		
Blennioidei Type B	*	*		
Blennioidei Type C			*	
Blennioidei Type D	*	*		
Blennioidei Type E	*	*	*	
Blennioidei Type F	*	*		
Brevoortia sp	*	*		
Chaenopsidae Type A				*
Clupeidae Type A	*	*		
Coryphopterus sp	*		*	
Coryphopterus glaucofraenum			*	
Ctenogobius saepepallens	*		*	
Doratonotus megalepis	*			
Eucinostomus lefroyi	*	*		*
Eugerres plumieri				*
Evorthodus lyricus			*	
Gobiesox punctulatus	*	*		
Gobiidae Type F			*	
Gobionellus boleosoma	*	*	*	
Gobionellus sp			*	
Gobiosoma sp	*	*		
Halichoeres sp		*		
Hypoplectrus sp	*	*		*
Jenkinsia lamprotaenia		*		
Jenkinsia parvula	*	*		
Labridae Type A		*		
Lycengraulis grossidens		*		
Malacoctenus sp			*	*
Monacanthus sp	*			*
Nes longus		*		
Pomacanthidae Type A	*	*		
Sardinella aurita	*	*		
Sparisoma sp	*	*		
Sphyraena barracuda				*
Stegastes diencaeus		*		
Strongylura notata				*
Syngnathidae Type A	*			*
Syngnathidae Type B	*			
Tripterygiidae Type A				*

However, four taxa are present across all three Regions: Blennioidei Type E, *Eucinostomus lefroyi*, *Gobionellus boleosoma* and *Hypoplectrus* sp. (Figure 8.2). Of these, *E.lefroyi* and *Hypoplectrus* sp. both decrease in density from Region 1 to Region 3. The decrease in density from Regions 1 through to 3 reflects the overall mangrove larval population per trap, which is significantly higher in Region 1 than Regions 2 and 3 (ANOVA: $F = 3.39$, $p = 0.035$).

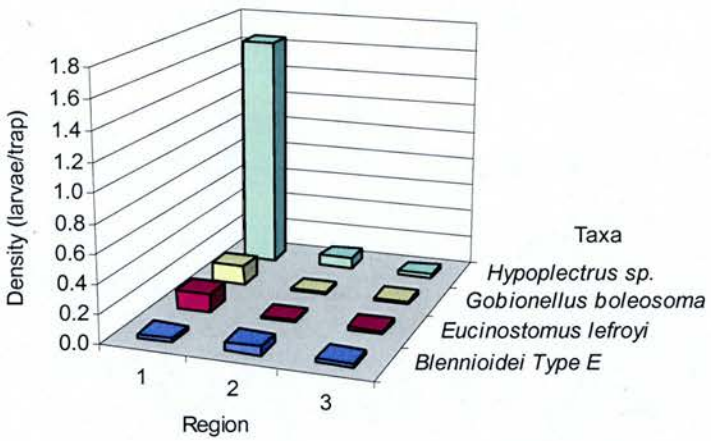


Figure 8.2. Mean larval density per light trap in the mangrove habitat of each Region, of taxa accounting for two thirds of dissimilarity between the night larval assemblages of each Region. A decreasing gradient is evident for *Eucinostomus lefroyi* and *Hypoplectrus* sp. from Region 1 through to Region 3.

The juvenile assemblage also varies significantly between Regions at the species level (ANOSIM: $R = 0.350$, $p = 0.007$). From a SIMPER routine it is evident that approximately two thirds of the dissimilarity between the Regional groups of the juvenile mangrove assemblages is accounted for by 19 out of the possible 34 taxa (Table 8.3). Of these, *Abudefduf saxatilis*, *Acanthurus* sp., *Haemulon flavolineatum*, *Lutjanus griseus, Scarus* sp. and *Strongylura notata* are present across all three Regions (Figure 8.3). All show a variation in abundance between the three groups, indicating that the abundance of taxa as well as their presence or absence is responsible for the clustering the juvenile mangrove assemblage into Regions. A decrease in density from Region 1, through Region 2 to Region 3, is evident for both *Haemulon flavolineatum* and *Lutjanus griseus* juveniles.

Table 8.3. Juvenile mangrove taxa accounting for approximately two thirds of dissimilarity between Regions, based on CLUSTER analysis at 85 % Bray-Curtis similarity. * denotes presence. *Abudefduf saxatilis*, *Acanthurus* sp., *Haemulon flavolineatum*, *Lutjanus griseus*, *Scarus* sp. and *Strongylura notata* are present across all three Regions, indicating that the abundance of taxa as well as their presence or absence is responsible for the groups shown.

Taxa	Region Groups		
	1	2	3
Abudefduf saxatilis	*	*	*
Acanthurus chirurgus	*		
Acanthurus coeruleus		*	
Acanthurus sp	*	*	*
Atherinomorus stipes		*	
Clupeidae Type A		*	*
Chaetodon capistratus			
Eucinostomus argenteus	*	*	
Gerreidae Type A	*		
Gerres cinereus			
Haemulon flavolineatum	*	*	*
Haemulon sciurus	*	*	
Halichoeres sp	*	*	
Lutjanus apodus			
Lutjanus analis	*		
Lutjanus cyanopterus		*	
Lutjanus griseus	*	*	*
Lutjanus jocu		*	*
Lutjanus mahogoni			
Ocyurus chrysurus			*
Pomacentridae Type A	*	*	
Scarus sp	*	*	*
Strongylura notata	*	*	*

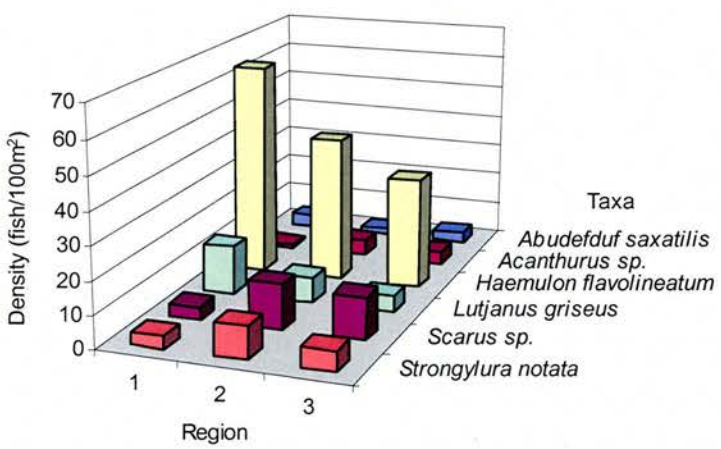


Figure 8.3. Mean density 100 m^{-2} in the mangrove habitat of each Region, of taxa accounting for two thirds of dissimilarity between the juvenile assemblages of each Region. A decreasing gradient is evident for *Haemulon flavolineatum* and *Lutjanus griseus* from Region 1 through to Region 3.

The adult mangrove assemblage shows no significant variation with Region, or Stations nested within Regions, indicating that adult presence or absence, or abundance, does not influence the larval and juvenile assemblages (ANOSIM: $R \geq 0.017$, $p \geq 0.068$). The structural complexity of the mangrove habitat, however, also differs significantly with Region, but not with Stations nested within Regions (ANOSIM: $R = 0.227$, $p \leq 0.001$; $R = 0.235$, $p = 0.093$ respectively). A gradient of complexity exists, from a low structural complexity in terms of prop-root density, length and relative length in Region 1 to a highly complex structure in Region 3.

The densities of larval *Eucinostomus lefroyi* and *Hypoplectrus* sp., and juvenile *Haemulon flavolineatum* and *Lutjanus griseus*, decrease from Region 1 to 3, indicating a link to the increasing complexity of the mangroves. Although a low structural complexity provides less shelter from predation, it allows greater access to prey. Size would therefore be expected to increase from Region 1 to 3, to lower the predation risk. The larvae of *E.lefroyi* and *Hypoplectrus* sp. do not show a marked variation in size distribution between the 3 Regions, however. In Regions 1 and 3, approximately 50 % of *E.lefroyi* larvae are 0.5-1.0 cm and 50 % 1.0-1.5 cm in length, with all larvae in Region 2 falling in the 0.5-1.0 cm size class. All *Hypoplectrus* sp. larvae are < 0.5 cm, regardless of Region.

The juveniles do show a marked variation with Region, however (Figure 8.4). Both *Haemulon flavolineatum* and *Lutjanus griseus* are present in 3 size classes of 5 cm intervals across the 3 Regions. The relative abundance of individuals present in the larger size classes increases from Region 1 through to Region 3, indicating a preference for high structural complexity in smaller, younger larvae, while older larger larvae are present in higher proportions in mangrove of low structural complexity.

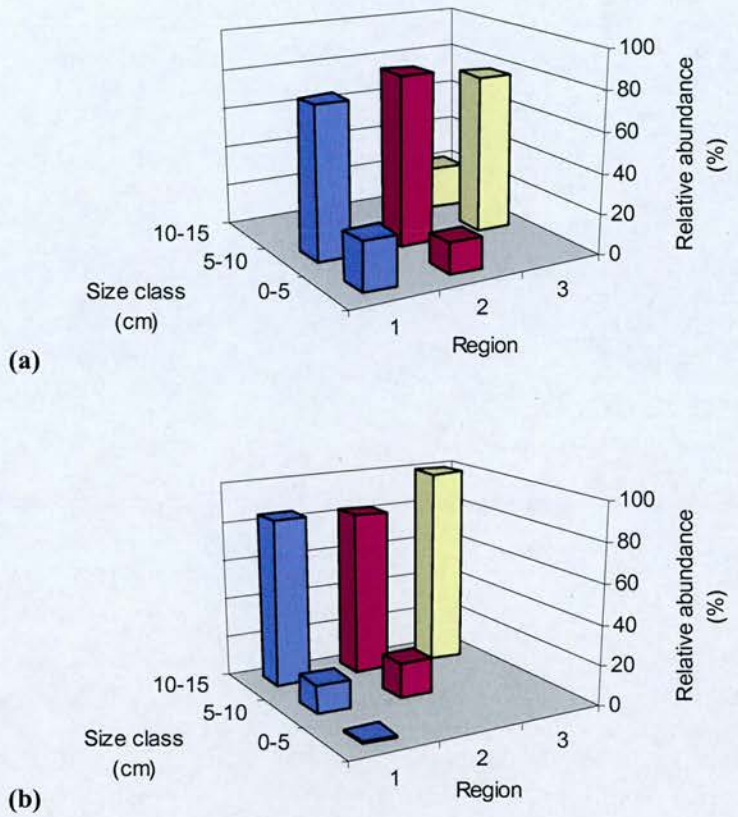


Figure 8.4. Relative abundance (%) of size classes of (a) *Haemulon flavolineatum* and (b) *Lutjanus griseus* juveniles in the mangrove habitat of Regions 1, 2 and 3. Calculated as proportion of species abundance in each Region. Both show an increasing proportion of larger juveniles from Region 1 through to Region 3.

Key findings

Variation in assemblage composition may be summarised as:

- a significant variation in assemblage composition is evident between Regions for both day and night larvae, and between Stations nested within Regions for the night larval assemblage;
- for the night larval collection, two thirds of the dissimilarity between assemblage composition by Station is accounted for by 45 out of a total of 73 taxa;
- for the day larval collection, two thirds of the dissimilarity between assemblage composition by Region is accounted for by 17 taxa, out of a total of 22

- the presence or absence of taxa, rather than the abundance, discriminates between Region groups within the mangrove day larval assemblages and Station groups within the night larval assemblages;
- Blennioidei Type E, *Eucinostomus lefroyi*, *Gobionellus boleosoma* and *Hypoplectrus* sp. are present across all 3 Regions in the night larval assemblage;
- the juvenile assemblage composition within the mangrove habitat varies significantly between Regions, but not between Stations nested within the Regions;
- the abundance of taxa as well as their presence or absence is responsible for the variation in juvenile assemblage composition between Regions;
- the abundance of *Haemulon flavolineatum* and *Lutjanus griseus* contribute to variation in the juvenile assemblage between Regions;
- the densities of *H.flavolineatum* and *L.griseus* decrease from Region 1 through Region 2 to 3, whereas the structural complexity of the mangrove habitat increases;
- the relative abundance of larger, older *H.flavolineatum* and *L.griseus* juveniles increases from Region 1 through Region 2 to Region 3.

8.2.2. Influence of abiotic variables on fish assemblages within the mangrove habitat

For the night larval population at the species level, correlation with the habitat structural parameters is maximised by the mean root length and the relative length of the roots (Table 8.4). At the family level the same parameters plus the root density are required to maximise the correlation. Mean root length varies significantly between each Region, and is therefore a potential influence on the larval assemblage composition (ANOVA: $F = 18.00$, $p \leq 0.001$). The Spearman rank correlation coefficients for the day larval assemblages and mangrove

Table 8.4. Summary of BIO-ENV analysis of environmental variables and habitat structural parameters against larval, juvenile and adult assemblages in the mangroves. * indicates variables that maximise the matching Spearman rank correlation coefficient between the environmental or structural parameter matrix, and the corresponding assemblage matrices at species and family level. † indicates significant variation with Region ($p < 0.05$). Larval assemblages collected at night by light trap and during the day by plankton net tow are analysed separately. The extinction coefficient and turbidity are of less influence in determining the assemblage composition than the other environmental variables, as neither maximises the coefficient. Mangrove prop-root length rather than water depth is most influential for the larval assemblages, whereas both are influential in the juvenile and adult assemblages.

	Night larva		Day larva		Juvenile		Adult	
	Species	Family	Species	Family	Species	Family	Species	Family
Environmental variable								
Water temperature (°C)	*	*	*	*	*		*	*
Extinction coefficient								
Wind velocity (m/s)	*		*					
Turbidity (FTU)								
Sulphate (mg/l)	*	*						
Nitrate (mg/l)		*			*	*	*	*
Salinity (‰)				*				
pH			*					
Correlation coefficient	**0.361**	**0.471**	**0.294**	**0.213**	**0.757**	**0.692**	**0.665**	**0.604**
Structural parameter								
†Water depth (m)					*	*	*	*
†Prop-root density (m^{-3})		*			*			
Prop-root length (m)	*	*	*	*	*			
Relative prop-root length (%)	*	*			*	*	*	*
Correlation coefficient	**0.746**	**0.787**	**0.027**	**0.047**	**0.676**	**0.644**	**0.528**	**0.527**

habitat parameters are all relatively low, so although prop-root length maximises the coefficient, its influence is very weak.

Correlation between the juvenile assemblage matrices and the abiotic data matrices are relatively high. The coefficient for the juvenile assemblage at species level and the environmental data is maximised by two of the environmental variables, water temperature and nitrate ion concentration. At the family level only nitrate ion concentration is required. For the structural parameters the mean water depth and relative root length maximise correlation at both the species and family level, along with the mean prop root density and length at the species level. The water depth and mean root length are both probable influences on the juvenile assemblage composition, as they vary significantly between each Region (ANOVA: $F = 14.37$, $p \leq 0.001$; $F = 18.00$, $p \leq 0.001$).

The Spearman rank correlation coefficients between the adult assemblage matrices and the abiotic data matrices are relatively high. For the structural parameters, the mean water depth and relative root length maximise correlation at both the species and family level. Water depth is likely to be influential due to its significant variation between Regions.

Key findings

The influence of abiotic variables on the fish assemblages of the mangrove habitat varies according to the life-stage being considered, and may be summarised as:

- the night larval, juvenile and adult assemblages all show a relatively strong correlation with water temperature, nitrate ion concentration and relative prop root length;

- the day larval assemblage correlation with the environmental variables matrices is very weak, indicating that other factors have more influence on the assemblage composition;
- water depth is a probable influence on the composition of the night larval and juvenile assemblages;
- mean root length is a probable influence on both the juvenile assemblage, and composition of the adult community.

8.2.3. Comparison of larval, juvenile and adult life stages within the mangrove habitat.

The adult, juvenile and night larval assemblages all show correlation between their composition and the variation in abiotic variables, in particular habitat structural parameters. The juvenile and night larval stages of individual taxa appear to be influenced by variation in habitat structural complexity. Individual taxa and life-stages are also likely to be of mutual influence on each other. Comparison of the spatial distribution of the different life-stages within each month shows a significant correlation between night larval abundance and juvenile density, and day larval abundance and adult density (Pearson correlation: $\rho \geq -0.686$, $p \leq 0.041$). This indicates a potential predator-prey correlation, with juvenile and adult predator densities reflecting larval prey abundance. Alternatively, the development of larvae into juveniles, and the production of larvae by spawning adults, may produce correlation between the respective stages. However, the adult and juvenile assemblages are distinct from the larval assemblages, based on taxonomical composition (Figure 8.5).

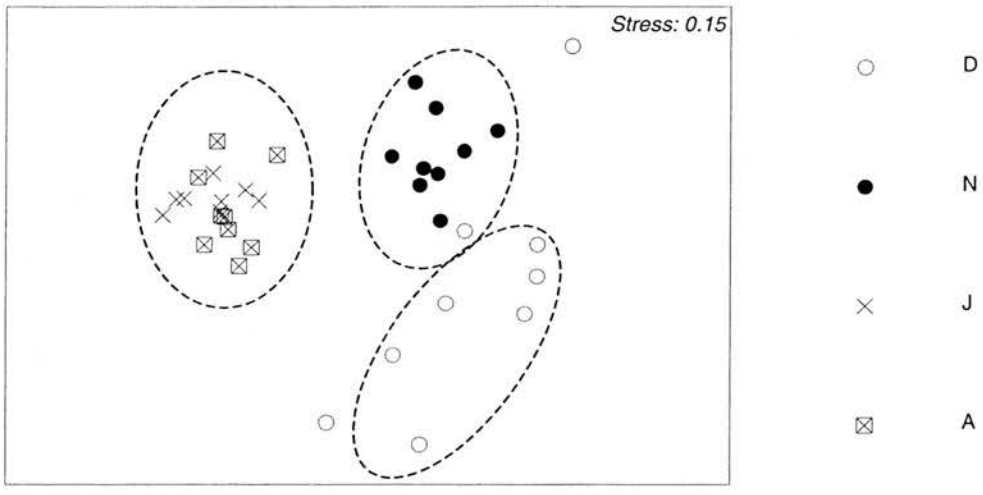


Figure 8.5. Non-metric MDS ordination plot by presence/absence composition of night larval (N), juvenile (J) and adult (A) mangrove assemblages recorded in each Station, and day larval (D) mangrove assemblages recorded along each transect. The juvenile and adult assemblages are grouped together at 40 % Bray-Curtis similarity, while the larval assemblages divide into the day and night collections.

All four groups differ significantly in terms of their assemblage composition (ANOSIM: $R = 0.723$, $p \leq 0.001$). According to a SIMPER routine, two thirds of the dissimilarity between the night larval, day larval and combined juvenile – adult assemblages in the mangrove habitat is due to 36 taxa out of a possible total of 112 (Table 8.5).

This indicates that a large proportion of each assemblage consists of rare taxa, with relatively few records at any life-stage. Of the discriminating taxa, 5 are present as larvae as well as juveniles and/or adults: *Atherinomorus stipes*, *Halichoeres* sp., *Sparisoma* sp., *Sphyraena barracuda* and *Strongylura notata*. This suggests that variation in the temporal and/or spatial distribution of the respective life-stages of these taxa is distinct. Indeed, only *Atherinomorus stipes* and *Strongylura notata* show any correlation in the distribution of their respective life-stages with time or space.

Table 8.5. The 36 taxa, out of a possible total of 112, accounting for approximately two thirds of dissimilarity between clustered night larval (N), day larval (D), and juvenile - adult (J&A) assemblages in the mangrove habitat, grouped at 40 % Bray-Curtis similarity. * denotes presence.

Taxa	Life-stage Group		
	N	D	J&A
Abudefduf saxatilis			*
Acanthurus sp			*
Atherinomorus stipes	*	*	*
Bathygobius curacao	*		
Blennioidei Type B	*		
Blennioidei Type D	*		
Blennioidei Type E	*		
Blennioidei Type F	*		
Brevoortia sp	*	*	
Chaetodon capistratus			*
Coryphopterus sp	*		
Ctenogobius saepepallens	*		
Eucinostomus argenteus			*
Eucinostomus lefroyi	*	*	
Gerres cinereus			*
Gobiesox punctulatus	*	*	
Gobionellus boleosoma	*		
Gobiosoma sp	*	*	
Haemulon flavolineatum			*
Haemulon plumieri			*
Haemulon sciurus			*
Halichoeres sp	*		*
Hypoplectrus sp	*		
Jenkinsia lamprotaenia	*	*	
Jenkinsia parvula	*		
Lutjanus apodus			*
Lutjanus griseus			*
Lutjanus jocu			*
Monacanthus sp	*	*	
Pomacanthidae Type A	*	*	
Sardinella aurita	*		
Scarus sp			*
Sparisoma sp	*		*
Sphyraena barracuda	*		*
Strongylura notata	*	*	*
Syngnathidae Type A	*	*	

The temporal variation of juvenile *S. notata* density shows a significant correlation with the night and day larval populations, while the juvenile and adult *A.stipes* correlate with each other, and with the night larval population, in terms of spatial variation (Pearson correlation: $\rho \geq 0.880$, $p \leq 0.049$). Therefore it is apparent that the dissimilarity between the night larval, day larval, juvenile and adult assemblages is not only due to the absence of individual taxa at one or more stages of their life

cycle, but also due to variation in the spatial and/or temporal distribution of different life-stages, where there is more than one present.

Key points

Comparison of the larval, juvenile and adult life stages within the mangrove habitat may be summarised as:

- the night larval abundance and juvenile density correlate significantly, as do the day larval abundance and adult density, indicating potential predator-prey correlation;
- the taxonomical composition of the juvenile and adult assemblages is distinct from the larval assemblages;
- two thirds of the dissimilarity between the night larval, day larval and combined juvenile–adult assemblages in the mangrove habitat is due to 36 taxa out of a possible total of 112;
- dissimilarity between the night larval, day larval, juvenile and adult assemblages is not only due to the absence of individual taxa at one or more stages of their life cycle, but also due to variation in the spatial and/or temporal distribution of different life-stages, where there is more than one present.

8.3. *Discussion*

The research question posed in the introduction is addressed by examining habitat complexity, as described in Chapter 2, and distribution patterns of larval, juvenile and adult reef fish. As the structure of a habitat becomes more complex, it provides more shelter from predators, but limits access to prey (Robertson & Duke, 1987; Thayer *et al.*, 1987; Robertson & Blaber, 1992; Al-Khayat and Jones, 1999).

Comparison of the assemblage composition of each stage (larval, juvenile and adult) in different areas of the mangroves shows

differential use of the mangrove habitat. A significant variation in assemblage composition is evident between Regions for both day and night larvae, and between Stations nested within Regions for the night larval assemblage. The presence or absence of taxa, rather than the abundance, discriminates between the day larval assemblages of each Region within the mangroves. In the case of the night larval assemblages, the presence or absence of taxa distinguishes the Station groups. In both cases, this indicates that rare species are principally responsible for the variation in assemblage composition.

In contrast, both the abundance and presence/absence of taxa discriminate between the night larval assemblages of each Region. A more even distribution of larvae in the water column may partly account for this, as larvae appear to show decreased levels of stratification at night (Choat *et al.*, 1993). Blennioidei Type E, *Eucinostomus lefroyi*, *Gobionellus boleosoma* and *Hypoplectrus* sp. are present across all 3 Regions in the night larval collections. Larval density may be expected to increase with habitat complexity, as more complex habitats have a potential for a higher interception rate of planktonic larvae (Robertson & Blaber, 1992; Baran & Hambrey, 1998; Nagelkerken, 2000). However, the density of *E.lefroyi* and *Hypoplectrus* sp. larvae decreases from Region 1 through to Region 3, whereas the structural complexity of the mangrove habitat increases. Both are generalised carnivores feeding mainly on invertebrates (Cervigón *et al.*, 1992), which are likely to be more accessible in habitats with low structural complexity (Hunter, 1981; Orth *et al.*, 1984). The increase of larval density with decreasing habitat complexity suggests that food availability is more important than the amount of shelter available. Neither species shows a marked variation in size distribution between the 3 Regions. As larger individuals may be expected to show a preference for more open habitat, being less vulnerable to predation, this also indicates that shelter availability is not of paramount importance.

The juvenile assemblage within the mangrove habitat also varies significantly in composition between Regions. Although the variation is principally accounted for by the presence or absence of taxa, the abundance of taxa is also responsible in part, indicating that variation in assemblage composition between Regions is not solely due to rare species. With reference to the research question, two species distinctive of the mangrove habitat have been selected for discussion: *Haemulon flavolineatum* and *Lutjanus griseus*. Recognised as inhabitants of the mangroves, young juvenile haemulids show an inverse correlation with predator abundance, while older juveniles do not (Tupper & Juanes, 1999). *H.flavolineatum* is a generalised, primarily nocturnal, carnivore, and rarely piscivorous (Randall, 1967). The juvenile stage of *L.griseus* is a distinctive mangrove predator, moving to outer reefs in the late juvenile or early adult stages (Ogden & Gladfelter, 1983; Parrish, 1989). Young *L.griseus* juveniles are generalised diurnal carnivores and usually present in seagrass beds, larger juveniles are predominantly nocturnal piscivores, especially of haemulids, and tend to enter the mangrove habitats at later stages (Randall, 1967; Starck, 1971; Hettler, 1989).

Juveniles of both *Haemulon flavolineatum* and *Lutjanus griseus* are present in all three Regions. As the two species have a potential prey-predator relationship, contrasting patterns of distribution may be expected. However, both decrease in abundance from Region 1 through to 3. In contrast, the structural complexity of the mangrove habitat increases from Region 1 through to 3, indicating a preference for low structural complexity by the juveniles of both species. Low structural complexity provides limited shelter but good access to prey, implying that the predation threat to *H.flavolineatum* and *L.griseus* is outweighed by prey availability, or access to prey.

The relative abundance of individuals present in the larger size classes of both species increases from Region 1 through to Region 3,

indicating a preference for high structural complexity in smaller, younger juveniles, while older larger juveniles are present in higher proportions in mangrove of low structural complexity. A relationship has often been noted between increased complexity and decreased incidence of predation in vegetated aquatic habitats (Orth *et al.*, 1984; Robertson & Blaber, 1992; Brewer *et al.*, 1995). The size distribution of both *H.flavolineatum* and *L.griseus* juveniles indicates that smaller individuals favour more complex habitats, which afford greater shelter and reduced risk of predation. This in turn reflects the predation pressure on the two species, which decreases with increasing size. In view of this, it seems appropriate to modify the earlier statement that the predation threat to *H.flavolineatum* and *L.griseus* is outweighed by prey availability, or access to prey, by limiting it to larger juveniles.

The adult mangrove assemblage shows no significant variation with either Regions or Stations, indicating that adult distribution is not influenced by variation in the complexity of the mangrove habitat. In addition, it suggests that no individual adult species has a marked influence on the use of the mangroves by the larval and juvenile assemblages. However, there is a significant correlation between the density of adults and larvae collected during the day, indicating potential predator-prey correlation. Nevertheless, the predation threat to selected species in the larval assemblage appears to be outweighed by food availability, as there is a general preference for lower habitat complexity in which food is more accessible. The same preference is apparent for the larger juveniles of *Haemulon flavolineatum* and *Lutjanus griseus*. The smaller juveniles are more vulnerable to predation, however, and display an apparent preference for more complex mangroves, in which shelter is greater but access to food is more limited. Many other fish species exhibit a strong association between small individuals and habitats with high structural complexity, with larger size classes moving to less complex areas (Thayer *et al.*, 1987).

Table 8.4. Summary of BIO-ENV analysis of environmental variables and habitat structural parameters against larval, juvenile and adult assemblages in the mangroves. * indicates variables that maximise the matching Spearman rank correlation coefficient between the environmental or structural parameter matrix, and the corresponding assemblage matrices at species and family level. † indicates significant variation with Region ($p < 0.05$). Larval assemblages collected at night by light trap and during the day by plankton net tow are analysed separately. The extinction coefficient and turbidity are of less influence in determining the assemblage composition than the other environmental variables, as neither maximises the coefficient. Mangrove prop-root length rather than water depth is most influential for the larval assemblages, whereas both are influential in the juvenile and adult assemblages.

	Night larva		Day larva		Juvenile		Adult	
	Species	Family	Species	Family	Species	Family	Species	Family
Environmental variable								
Water temperature (°C)	*	*	*	*	*		*	*
Extinction coefficient								
Wind velocity (m/s)	*		*					
Turbidity (FTU)								
Sulphate (mg/l)	*	*						
Nitrate (mg/l)		*			*	*	*	*
Salinity (‰)				*				
pH			*					
Correlation coefficient	**0.361**	**0.471**	**0.294**	**0.213**	**0.757**	**0.692**	**0.665**	**0.604**
Structural parameter								
†Water depth (m)					*	*	*	*
†Prop-root density (m^{-3})		*			*			
Prop-root length (m)	*	*	*	*	*			
Relative prop-root length (%)	*	*			*	*	*	*
Correlation coefficient	**0.746**	**0.787**	**0.027**	**0.047**	**0.676**	**0.644**	**0.528**	**0.527**

9.0 General discussion and conclusions

9.1 *General discussion*

Although Calabash Cay lies within the lagoon of Turneffe Atoll, it is only a few 100 m from the reef crest, and channels in the outer reef are present to the north, east and south of the island. Therefore the migration of fish to and from the mangrove habitat of Calabash occurs from several directions. A nested sampling design has been used in the present study, in order to provide sufficient coverage of the mangroves and seagrass beds to capture a good representation of immigration and emigration patterns.

The two methods used to sample larvae in the present study appear complementary, with a significant difference in taxonomic composition between the respective collections. However, as nets were used during the day and light traps at night, diel migration patterns are also likely to have contributed to the differences between the two (Leis, 1991). Nevertheless, earlier studies have shown the two methodologies to differ significantly in catch composition when used simultaneously (Choat *et al.*, 1993; Brogan, 1994; Hickford & Schiel, 1999). Therefore, it is assumed that the use of the two methods has provided a wide range of the diurnal and nocturnal larval taxa present. In addition, the use of more than one size of plankton-net for each tow, and therefore more than one mesh-size, permitted the collection of a wide size range of larvae.

A relatively new and evolving sampling method, the light trap collections were comparable to other studies in the Caribbean, with the families Atherinidae, Clupeidae, Gobiesocidae, Gobiidae, Labrisomidae, Monacanthidae, Pomacanthidae, Scaridae and the suborder Blennioidei comprising the most abundant groups throughout (Rooker *et al.*, 1996; Sponaugle & Cowen, 1996b; Watson *et al.*, 1999; Watson *et al.*, 2002). The abundance of the most dominant species

varies however, with 79 % of the collections made by Rooker *et al.* (1996) dominated by clupeids. By contrast, Sponaugle and Cowen (1996b) reported that 65 % of all collections consisted of atherinids. Atherinidae also dominate the present study but at a much lower proportion of 14 %. Watson *et al.* (1999; 2002) report both as being dominant in collections but do not state abundances. As both families school in nearshore surface waters, they are more disposed to collection by light-traps, which sample surface waters.

Absolute differences in abundance between the present study and others in the Caribbean are likely to be primarily due to habitat differences, with the latter mainly conducted over coral reefs. Sponaugle and Cowen (1996b) suggest that variation in atherinid abundance is most likely due to variation in relative light intensity between traps. Supporting this are the results of Gehrke (1994), which demonstrate increased phototaxis in 2 fish species with increasing light intensity, regardless of wavelength. Although it has rarely been cited as such, light intensity is likely to be a significant source of variation between different studies, in addition to factors such as geographic region, habitat, depth, time and trap-structure. As there was no significant difference in the abundance of larvae collected by traps in the present study, it is assumed that their light intensity was comparable and therefore not a source of variation.

Low abundances in light trap collections are frequently recorded, and are generally attributed to a lowered light attraction response and increased predation pressure (Rooker *et al.*, 1996; Hickford & Schiel, 1999). The effectiveness of light-aggregation devices is lessened due to the increase in background underwater light intensity from a full moon, while predation risk is often reduced during moonless nights.

The taxonomic composition of light-trap collections and plankton-net tows is considered to be method dependent, primarily due to selectivity

for positively phototaxic species in the former and net avoidance in the latter (Gregory & Powles, 1988; Choat *et al.*, 1993; Brogan, 1994; Doherty *et al.*, 1994; Thorrold *et al.*, 1994; Rooker *et al.*, 1996; Sponaugle & Cowen, 1996a, 1996b; Hickford & Schiel, 1999; Fisher & Bellwood, 2002). The low number of light-trap studies to date necessitates comparison between locations separated by large distances, which may lend a significant inherent variation to observations, such as the dominance of certain families or the total absence of families.

Atherinid larvae have the highest overall abundance both in the present study and that of Sponaugle and Cowen (1996b) in Barbados. Rooker *et al.* (1996) found Clupeidae dominated larval collections in Puerto Rico, yet they were absent in Barbados (Sponaugle & Cowen, 1996b) and only the 9th most abundant family in Belize. Fisher and Bellwood (2002) and Choat *et al.* (1993) found clupeids dominant at Lizard Island, as did Hair (2000) in the Solomon Islands and Brogan (1994) in the Gulf of California. In many of these studies, clupeids have been excluded from further analysis due to their significant abundance. However, they merit further study to establish whether behavioural differences account for their level of dominance, such as the observation of Thorrold *et al.* (1994) that the abundance of clupeids collected in moored plankton nets in the Bahamas peaked at the full moon in contrast to most other taxa.

Comparison of larval studies is further complicated by a lack of consideration of such physical influences on the larval input into shallow-water habitats. Rather, physical attributes of the habitats are considered most important in determining the distribution of larvae (Blaber & Blaber; 1980; Dennis, 1992; Kramer *et al.*, 1997; Holbrook *et al.*, 2000). This is largely due to the difficulty in separating environmental factors, such as lunar and tidal periodicity. Although a wide range of abiotic variables were measured in the present study, not

all physical characteristics of the water column were examined quantitatively. Tidal velocity may vary both horizontally and vertically in the water column, and the ability of larvae to orientate themselves accordingly will influence both their speed and direction of travel (Heath, 1992; Cowen & Sponaugle, 1997; Stobutzki & Bellwood, 1997; Fisher & Bellwood, 2000, 2002; Fisher *et al.*, 2000; Leis & Carson-Ewart, 1999; Armsworth *et al.*, 2001). Around Calabash Cay itself, tidal velocity is unlikely to show a high degree of spatial variance, as the island is very small and the water immediately surrounding it is well circulated. The turbulence of the water may also vary, especially in shallow-water habitats where vegetation will influence patterns of water flow. Both turbulence and tidal velocity will influence the initial interception of larval pulses by vegetated habitats, however, as will the size and frequency of larval pulses.

The spawning of marine fish has often been linked to water circulation patterns, with adults migrating to sites that offer enhanced survival to their larvae through transport to suitable nursery sites (Johannes, 1978; Heath, 1992). In the present study, the night larval, juvenile and adult assemblages all show a relatively high correlation with the environmental variables and habitat structure parameters measured, whereas the day larval assemblage does not. The taxonomic composition of the juvenile and adult assemblages is distinct from the larval assemblages. This dissimilarity is due both to the absence of individual taxa at one or more stages of their life cycle, and also to variation in the spatial and/or temporal distribution of different life-stages, where there is more than one present. The seagrass and mangrove habitats are both of importance for different life stages of many species, and as such should be considered as a continuum.

However, mangrove stands and seagrass beds do not constitute the only shallow-water habitats present in the Caribbean, and it would be inappropriate to consider them in isolation. Open sand and mudflats

are additional habitat types that often present in close association to mangroves and seagrass. An immediate point of comparison is that while seagrass and mangroves are vegetated habitats and therefore have a high degree of structural complexity, the potential for providing shelter through complex structures is more limited in areas of open sand and mudflats. However, both offer greater prey accessibility to general carnivores that feed on benthic invertebrates, and visual predators such as *Sphyraena barracuda*, than vegetated habitats (Blaber & Blaber, 1980; Orth *et al.*, 1984). Shelter from visual predators is not only provided by complex habitat structures. Turbid water is often presented as an effective refuge from predation, and along with uneven substrate such as sand ridges provides alternative protection to prey species (Moore & Moore, 1976; Minello *et al.*, 1987; Robertson & Blaber, 1992; Mitsch & Gosselink, 1993; Laroche *et al.*, 1997; Whitfield, 1999; Macia *et al.*, 2003).

A comparison of species in the shallow-water habitats of Caribbean islands with and without mangroves and seagrass by Nagelkerken *et al.* (2000a) included *Haemulon flavolineatum*, *Lutjanus griseus* and *S.barracuda*. No significant difference in the density of *H.flavolineatum* was apparent between the two island types, and as a general carnivore it can utilise a wide range of habitats. *L.griseus* and *S.barracuda* were only found on islands with mangrove and seagrass habitats. Both species are piscivores, however, and therefore are to be expected in habitats with high fish concentrations, such as those offering extensive shelter in the form of complex structures.

In the present study *Haemulon flavolineatum* shows a dependence on the mangrove habitat, principally for shelter as young juveniles and for food as older juveniles. However, in the study of Nagelkerken *et al.* (2000a), a low level of dependence on vegetated habitats is apparent. The degree to which coral reef fish species rely on individual habitats varies extensively as shown by this example, and the ecology of each

species merits consideration when examining distribution patterns, in addition to physical attributes of the habitat itself.

The three hypotheses presented in the original research rationale of Chapter 1 put forward food accessibility, shelter availability and predation pressure as three respective principal explanations of the importance of mangroves and seagrass beds as nursery habitats. However, the present study has shown that these hypotheses are not mutually exclusive, and fish are attracted to these habitats due to a combination of greater food availability, heterogeneous structural complexity and reduced predation.

The results presented in Chapters 3-8 show how varied the role of individual aspects of habitats can be when considering the ecology of different species, and their separate life history stages in turn. Not least, the high number of coral reef fish taxa present in the shallow-water habitats of Calabash Cay as larvae and juveniles indicate that they are of importance to a wide range of species as nursery grounds. No other study to date has presented such a conclusive list of larval species to be found in the mangrove and seagrass habitats of Turneffe Islands atoll and Belize as a whole.

The two main factors commonly used to explain the distribution of early life history stages of fish, shelter and food availability, are both shown to be influenced in turn by the structure of the mangrove and seagrass habitats. The description of ontogenetic shifts in habitat use shows how the variation in structural complexity of the mangrove and seagrass habitats is exploited as the needs of larvae, juveniles and adults change during their development.

In addition, variation in abiotic factors other than habitat structure are shown to be influential in fish distribution, in particular the turbidity and the light attenuation coefficient of the water column, although both

are influenced in turn by habitat structural complexity. Both are of influence by reducing the efficiency of visual predators, thus reducing predation risks. Although often quoted as influential aspects of vegetated shallow-water habitats, these two factors are rarely measured in association with fish distribution (Mitsch & Gosselink, 1993; Laroche *et al.*, 1997; Whitfield, 1999; Macia *et al.*, 2003). Another aspect rarely considered quantitatively is the short-term temporal scale of larval supply, which the present study examined over hours, days and weeks. No significant difference was apparent due to the time of night at which light-trap samples were taken, a factor often assumed by previous studies but not demonstrated quantitatively (Holmes & O'Connor, 1988; Watson *et al.*, 2002). The variation observed over days and weeks is attributed to lunar and tidal periodicity, and larval pulses, as suggested in earlier, similar studies (Thorrold *et al.*, 1994; Doherty *et al.*, 1994; Rooker *et al.*, 1996; Sponaugle & Cowen, 1996a, 1996b; Kingsford & Finn, 1997; Hickford & Schiel, 1999).

Many of the taxa recorded are of direct economic value, either as fishery species or potentially for the aquarium trade. They are also of indirect value to tourism, already Belize's largest industry and a rapidly growing section of the economy. The large number of larval and juvenile taxa illustrates the importance of the mangrove-seagrass system of Calabash Cay as a transient habitat for many reef species, and with Belize's mangrove stands alone covering 78,511 ha it merits a greater degree of structured management than set out at present. In Belize City alone, mangrove clearance over the last decade has accounted for a 0.7 % reduction in the national total (Murray *et al.*, 2003).

To stem the continuing destruction of shallow-water habitats for aquaculture and coastal settlement development, and the over-exploitation of wood and fisheries resources, stronger enforcement of existing legislation is required. To this aim, studies such as the present

one provide invaluable information to authorities charged with protecting the marine environments, by establishing which areas are of importance in the life cycles of reef fishes, and therefore require active protection. Most of the Turneffe Islands atoll is not protected by legislation, and as a well-known fishing and scuba-diving site it is vulnerable to exploitation by the growing tourism industry. At the very least, it is proposed that full studies of marine fauna should be conducted prior to any further development on its constituent cays. A precedent for this has been established by the present study. In view of the high diversity of fish present in early life history stages at Calabash Cay, it is suggested that the marine reserve status of the northern Vincent's Lagoon requires reviewing to encompass other, non coral reef habitats in the atoll. The large area of the atoll and its orientation are likely to result in marked variation of environmental parameters and reef fish assemblages between cays, and a resulting variation in the need for management and protection measures. By affording conservation status to established nursery areas such as Calabash Cay, the ability to maintain the extensive marine resources of the atoll at present day levels will be maximised.

9.2 *Conclusions*

The reef fish assemblage of the mangrove and seagrass habitats of Calabash Cay relates closely with other Caribbean studies in terms of taxonomical composition, and is composed of both transient and resident taxa. Approximately 50 % of the taxa appear to be obligate mangrove or seagrass residents, although many are rare and therefore under-represented.

Larval supply is high to both habitats, with higher rates of settlement apparent in the seagrass, explained by the greater degree of shelter offered by the fine structure of the seagrass plants compared to the mangrove prop roots. Nevertheless, similar taxa dominate in the two habitats.

Subsequent decrease in diversity to the juvenile assemblage is explained by settlement to cryptic stages, natural mortality and emigration. Separation of taxa between the two habitats is more pronounced in the juvenile assemblage, indicating active settlement and migration patterns. Several species show differences in feeding strategies with age, sometimes reflected in variations in distribution. Susceptibility to predation also varies with age, and again influences spatial distribution.

This is also evident in the distribution of adults, which for some taxa contrasts with juveniles, showing differences in habitat use and feeding strategies. All three stages show species- and size-specific patterns in habitat use, in particular relating to the structural complexity of the habitat. Spatial variation with environmental factors is also evident for all stages, especially by size.

Larval density and assemblage composition is correlated with the water turbidity and extinction coefficient.

Lunar periodicity in larval supply is apparent, with greatest density and diversity occurring during the three-quarter moon. The time of night at which light traps are deployed has no significant effect on the larval collection, but sample composition showed significant variation between successive nights, indicating strong larval pulses.

Variations in density values suggest that most larvae are supplied to the mangroves initially, but settle into the adjacent seagrass where they develop into juveniles, moving to the mangroves towards the end of the juvenile phase. Development to adulthood is completed in the mangroves and followed by migration to coral reef habitats.

A high level of ontogenetic migration is evident between the seagrass and mangrove habitats, indicating that both are of relative importance in the life cycles of several reef fish taxa and merit consideration as a single continuous unit. The shelter provided by habitats seems of most importance to the small and young stages of each phase, more vulnerable to predation pressure, while prey availability is more important to larger and older stages.

Turneffe Islands atoll is not only the largest atoll in Belize, but also in the western hemisphere, and therefore is indisputably important. The extensive mangrove cover on the islands sets it apart from its sister atolls in the Caribbean Sea. Largely unexploited until recent years, Turneffe runs the risk of becoming developed and degraded before adequate management is in place. The high diversity of coral reef fish found in the present study alone shows that both the mangrove and seagrass habitats of Calabash Cay are of consummate importance, and demands stratified management initiatives to maintain a balance between development and conservation on the atoll.

10.0 References

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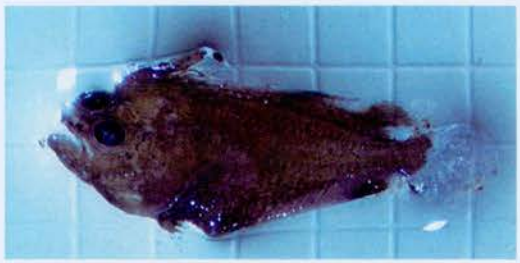
Appendix 3.2. Representative images of larval stages of coral reef fish collected from the mangrove and seagrass habitats of Calabash Cay, 2000-2001.

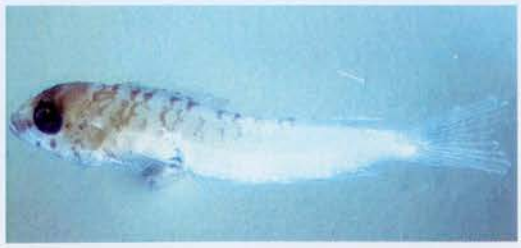


Achirus lineatus

Apogon sp.

Apogon sp. (BL 5 mm)

Atherinomorus stipes (BL 11 mm)



Parablennius marmoreus (BL 12 mm)

Blennioidei Type A

Blennioidei Type B

Blennioidei Type C

Blennioidei Type D

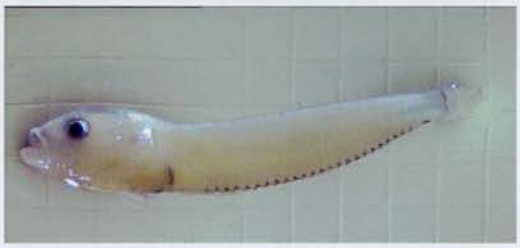
Oligoplites saurus

Chaetodon sp. (BL 5 mm)

Carapus bermudensis (BL 160 mm)

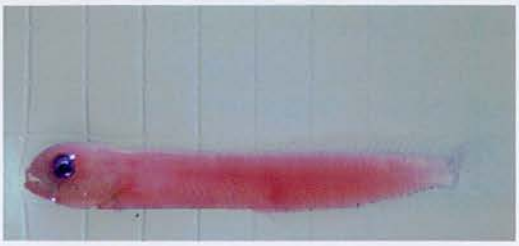
Jenkinsia lamprotaenia

Brevoortia sp.

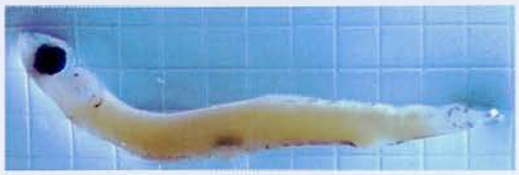


Acanthemblemaria chaplini

Gillellus jacksoni



Stathmonotus stahli tekla



Anchoa lamprotaenia

Anchoviella perfasciata

Exocoetidae Type A

Coryphopterus glaucofraenum (BL 6 mm)

Diapterus auratus (BL 9 mm)

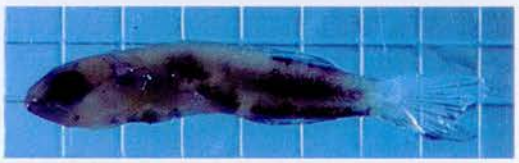
Coryphopterus sp.

Diapterus rhombeus

Evorthodus lyricus (BL 10 mm)

Eucinostomus plumieri

Gnatholepis thompsoni

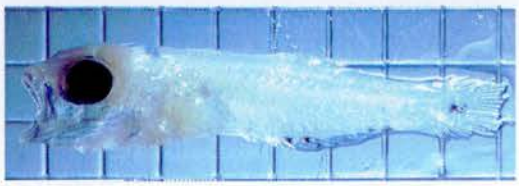


Bathygobius curacao

Gobiosoma bosci

Bathygobius soporator (BL 7 mm)

Nes longus (BL 12 mm)



Haemulon sp.

Doratonotus megalepis (BL 7 mm)

Monacanthus setifer (BL 9 mm)

Holacanthus tricolor

Stegastes diencaeus (BL 9 mm)

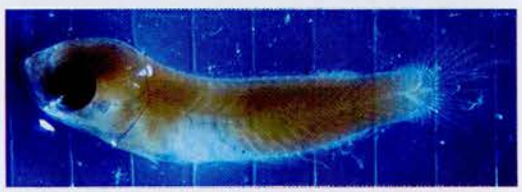
Scarus sp.

Sparisoma sp. (BL 8 mm)

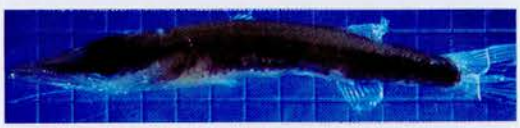
Scorpaena sp.

Hypoplectrus sp.

Hypoplectrus sp. (BL 8 mm)



Sparidae Type A



Sphyraena barracuda

Synodus sp. (BL 12 mm)

Sphoeroides maculatus (BL 7 mm)